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Biology of Mixed Foraging Flocks of Avian Species.

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BIOLOGY OF MIXED FORAGING FLOCKS OF AVIAN SPECIES

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ABSTRACT

The ecology and behavior of selected mixed bird flocks were studied, to determine what advantages may be gained from flock participation. Observations were conducted in Louisiana, Maine, and Costa Rica. Several habitats were studied in each region. Special emphasis was placed upon evaluation of already hypothesized ideas of flock function.

Among woodland birds protection from predation probably is a relatively unimportant advantage gained from flocking. However, alarm systems are widespread through flocks. The elaborate development of these mechanisms suggests a past or potential protective function.

Some species that are territorial in the breeding season may become intraspecifically gregarious under severe environmental conditions. These may include the flock leaders, the passive nuclear species of the flock. If flock leaders such as Carolina Chickadees and Tufted Titmice are territorial, as in Louisiana, the foraging range of nonterritorial associates may be restricted, unless they meet other flocks and continue on.

Characteristics of Louisiana flocks found in areas supporting the lowest avian populations included larger

numbers, greater spacing between flocks, and a stronger tendency for flocking species to be associated with these groups.

In most cases where closely related species occur together, a strong tendency for reciprocity in foraging was noted. Such reciprocity was found between Carolina Chickadees and Tufted Titmice. In an area where Black-capped Chickadees are the only representative of the genus, a wider spectrum of foraging occurred, probably as a result of the absence of close competitors. When flocking together, Brown-headed Nuthatches and Pine Warblers exhibit different foraging patterns from those that they employ when alone.

Where no reciprocity exists, a strong tendency for hostile behavior occurs, as in kinglets. In most winters the two species (Golden-crowned and Ruby-crowned) are only narrowly sympatric. Many warblers in fall flocks are very aggressive, perhaps as a result of their close relationship and of traces of breeding behavior remaining. Dull plumage may reduce hostility at this time.

Superabundance of a single food may increase the hostile behavior, because of increased contact with other individuals resulting from a change in foraging methods. Flock participation dwindles somewhat during superabundance, at least in Brown-headed Nuthatches.

Longleaf Pine is a sporadic producer of seeds, and it could not serve as an effective limiting factor for sedentary species, though many mixed flock members feed heavily upon the seeds.

Variation in stomach contents was usually closely correlated with the areas in which birds were observed foraging. However, even when pine seeds were the major part of their diet, some species spent a surprising amount of time foraging on limbs, on trunks, and in foliage. Considerable variation occurs in stomach contents of a species in one area.

The speed with which flocks moved usually varied directly with the size of the flock. Seldom did flocks move over fixed routes. They wandered about within a restricted area. Presence in a flock usually restricts a species to the part of the habitat that it forages most efficiently.

Mechanisms exist that serve to regulate the numbers of a species in a flock. Some species such as the Black-capped Chickadee (usually semi-sedentary in winter) will increase their hostile behavior when unusually large numbers of their species are present. Others, such as Myrtle Warblers, increase their movement out of mixed flocks with their rise in number and then tend to wander extensively.

Several attributes favoring gregariousness are characteristic of the species of which flocks are comprised. These include dull plumage, low hostility, possession of notes that attract other species, and suppression of song.

The tendency to flock is an efficient group adaptation that cuts broadly across the lines of avian classification.

INTRODUCTION

Groups of small birds comprised of two or more species are a familiar sight in many parts of the world. While such flocks have attracted most attention in tropical regions many species (notably some of the Paridae) may be observed flocking within the temperate zones. In spite of the conspicuousness of these groups, relatively little intensive study has been devoted specifically to them, a notable exception being Moynihan's (1962) work on some tropical flocks. Paradoxically, less study has been devoted to temperate flocks than to tropical ones.

Mixed flocks have been recognized for many years, and such workers as Bates (1864) in the Amazon and Belt (1874) in Nicaragua described them in some detail. More recent papers dealing with mixed flocks in addition to Moynihan's include those of Davis (1946) in Brazil, Short (1961) in Mexico, Willis (1960) in British Honduras, Swynnerton (1915) and Winterbottom (1943, 1949) in Africa, Stresemann (1917) in the East Indies and Germany, and Gannon (1934) and Hindwood (1937) in Australia. Rand (1954) dealt with the general problem of social feeding behavior in birds. Several other papers not dealing solely with this phenomenon are of importance.

As indicated above, Moynihan's paper is the most ambitious study yet made on mixed flocks, but it deals nearly exclusively with the behavior of a few tropical flocks in Panama. Hence, the value of additional work on this phenomenon is evident.

MATERIALS AND METHODS

Flocks were intensively studied in three widely separated geographical areas. During the summers of 1962 to 1964 I devoted considerable time to investigating the flocks on Hog Island, a part of Bremen, Lincoln Co., Maine, lying a short distance off the coast. The island is largely spruce-clad (*Picea rubens* and *P. glauca*), except for one area of several acres consisting principally of White Birches (*Betula papyrifera*), which was the subject of intensive study. The stands of spruce on the island, as well as the mixed coniferous-deciduous forests of the surrounding mainland, were studied more briefly.

Observations were made at and around Webster, Androscoggin County, Maine for parts of several winter years, extending from 1957 to 1964. Work here was also conducted in mixed coniferous-deciduous woodlands.

During the fall and winter of the 1963-64 and 1964-65 seasons flocks were studied intensively at three locations in Louisiana, with supplementary observations being made in other areas. The principal study areas included:

1. Mature deciduous forest four miles south of Louisiana State University, East Baton Rouge Parish.

This is a low flat woodland partially flooded for a considerable part of the fall and winter by a few inches of water. The most important species of trees include Nuttall Oak (Quercus Nuttallii), Sweet Gum (Liquidambar styracifolia), and Hackberry (Celtis occidentalis). American Hornbeam (Carpinus caroliniana) is an important member of the understory, and blackberry (Rubus sp.) and Dwarf Palmetto (Sabal minor) are sporadically prominent in the usually sparse ground cover.

2. Mixed pine-deciduous forest three miles northeast of Satsuma, Livingston Parish. Large parts of this area are also flooded during much of the fall and winter. This area contains a deciduous forest in the lower parts, and tall pines grow in the parts with slight elevation. The principal deciduous species is Water Oak (Quercus nigra); but scattered Southern Magnolia (Magnolia grandiflora), Beech (Fagus grandifolia), and Chestnut-oak (Quercus Prinus) occur. American Hornbeam (Carpinus caroliniana) is extensive in the understory. Dwarf Palmetto (Sabal minor) is the most prominent species in the ground cover. On the slightly higher ground, Loblolly and Spruce Pines (Pinus taeda and P. glabra) predominate. The tree cover in this area is about 50 per cent coniferous and 50 per cent deciduous.

3. Longleaf Pine forest three miles west of Fluker, Tangipahoa Parish. This is a pure stand of Longleaf Pine (Pinus palustris), with Blackjack Oak (Quercus marilandica) forming a scattered understory.

I spent the period from late February to late April, 1964, in Costa Rica, attempting to obtain comparative data on some tropical flocks. Areas studied included the following: an abandoned coffee plantation with tall shade trees at the Universidad de Costa Rica, San Jose Province (1000 m); a subtropical moist forest in the Tilaran region, Auanacaste Province (800 m); a high montane oak forest and second-growth scrub vegetation about La Georgina, San Jose Province (3000 m); and a tropical wet forest at Rincon de Osa, Puntarenas Province (sea level).

Extensive notes were taken on the flocks while in the field. Observations were facilitated by use of a pair of 7X50 binoculars.

Most mixed flock studies have been of an ecological or behavioral nature, or have consisted of simple general description. Realizing the dearth of comparative ecological-behavioral data, I decided early in the study to concentrate upon this aspect.

Many problems arise in studying flocks. Exhaustive effort is required to mark a population satisfactorily by capture and banding. In order to insure that density and forage patterns would not be altered, baiting was not

practiced. Nets were used in an attempt to capture flock members, but because of the difficulty involved in capturing sufficient numbers of these tree-foraging birds, many of which do not regularly descend to lower levels, this part of the project was abandoned. An unsuccessful attempt was made to utilize tree-level nets.

The taller vegetational associations at Baton Rouge and Satsuma, Louisiana, proved somewhat difficult to study on occasions when the light was poor and the birds were in the treetops. In these circumstances identifications were sometimes impossible. Less difficulty was experienced in the Longleaf Pine forest, which was not nearly as tall.

During many hostile displays it was impossible to determine which bird was the instigator and which the attacked individual, or to identify both as to species; thus, the actual recorded data represented only a small fraction of the actual observations.

Many specimens were taken on areas in the general vicinity of the Louisiana study plots for stomach analysis. All collecting was done at least one-half mile from a study area, in order to lessen the possibility of disturbing the population density.

DEFINITIONS

Though defined in many ways, flocks in this account will be considered as any group of two or more birds brought together by some sort of social bond, other than sexual. The bond may be either one-sided or reciprocal. On the other hand, congregations may include any gathering of two or more birds at an external environmental element such as foods, water, or ants; but involve no further behavioral reactions. Johnson (1954) found that with few exceptions mixed flocks were distinct from those forming "anting congregations" in Panama. Any nonreproductive grouping might be considered an aggregation. Flocks as here defined have been identified elsewhere in the literature as societies, parties, or bands.

A number of attempts to identify the status of flock members have been devised (Winterbottom, 1943, 1949; Davis, 1946; Moynihan, 1962). In practice it is very difficult to strike upon a single simple system satisfactory for classifying the roles that members take in flocks. To compound the problem, the role of a species may vary geographically, seasonally, or with the species composition of a flock.

Nevertheless, some attempt at classifying the members of these gatherings is necessary. Moynihan's (1962) modification of the terminology of the earlier papers proves valuble in this respect. Following Winterbottom (1943), he separates flock members into nuclear and attendant species. Moynihan defines nuclear species as species whose behavior helps appreciably to stimulate formation of mixed flocks or to maintain their cohesion. Attendants supply little but their presence. There is no clear line of differentiation between these two categories. Moynihan has made a further useful distinction, separating passive nuclear and active nuclear flock members. Passive nuclear species are those that are followed or joined by other species more frequently than they follow or join other species. Active nuclear species follow or join other species more often than they are followed or joined by other species. Though species that are over-all passive nuclear in their reactions may be active nuclear in their relation to some flock members (such as the relation of the Carolina Chickadee to the Tufted Titmouse described later), the distinction is still a helpful one.

EFFECTS OF WEATHER

Weather exerts definite modifying effects upon the foraging of mixed flocks.

Hard rain definitely slows down the activity of foraging flocks, though light rain has less effect. Wet foliage itself appears to have as much influence upon the rate of activity as the actual light rain.

Wind is more instrumental in curtailing flock foraging activity than light rain; it drives the individuals down into lower strata and brings them closer to one another than they would otherwise be. The result is maximum contact between individuals in the flock and with the ground-inhabiting species as well. On 29 August 1962 a flock on Hog Island was observed foraging actively at a low level sheltered from a heavy wind of 20-35 mph. The members were much closer to each other than they would be under normal circumstances. Usually flocks ranged up to 50-55 feet when foraging in this area, but this group seldom ventured over 15 feet on this windy day. In addition to such species as Black-capped Chickadees and Golden-crowned Kinglets this flock included such arboreal forms as Red-eyed Vireos, Bay-breasted

Warblers, Blackpoll Warblers, and American Redstarts as well as members of the ground stratum such as Winter Wrens, Northern Waterthrushes, Yellowthroats, and White-throated Sparrows. Seldom does this combination of species intermingle so thoroughly.

Unusually low early morning temperatures (below approximately 30°F) often resulted in a somewhat diminished early morning activity in some members of the Louisiana flocks and a tendency when possible to perch in the sun, activity increasing slightly later in the morning. Carolina Chickadees were especially prone to sun in this manner. This phenomenon has been noted in Black-capped Chickadees by Lawrence (1958) far to the north in Ontario, and it perhaps results in a more favorable energy balance than might otherwise be obtained. On warmer mornings Carolina Chickadee activity would be correspondingly greater in the early hours.

In Illinois, Johnston (1942) noted that when temperatures ranged above 25°F, flocks tended to spread out and scatter over the forage area. She noticed no effect attributable to sun or rain but found that strong wind caused the individuals to seek shelter. Her studies were conducted on Downy Woodpeckers, Black-capped Chickadees, Tufted Titmice, and White-breasted Nuthatches.

Presence of snow cover may alter foraging patterns in the Great Tit (Hartley, 1953). Most regular winter

species are so adapted that they are not heavily dependent upon sources made inaccessible by snow (Kendeigh, 1934). I found that a moderately falling snow appears to increase the foraging activity of Black-capped Chickadees in Maine.

High temperatures hasten reproductive behavior and unseasonably early warm weather may result in the temporary breakup of flocks in Maine and Louisiana.

Weather is an important factor in the build-up and abundance of migrants within the fall flocks. If several consecutive nights unsatisfactory for migration occur, numbers will build up substantially within the richer feeding areas, such as the birches on Hog Island. The numbers usually decrease following a night of heavy migration, though new migrants will appear. Mayfield (1937) noted that in Tennessee, cool weather often marked the break-up of one flock and the subsequent formation of another.

COMPOSITION OF FLOCKS

Mixed insectivorous flocks are loosely knit organizations. Nevertheless, certain vocal patterns of passive nuclear species will consolidate these groups to some degree.

Associations are frequently changing in mixed flocks, though some members remain together for considerable periods of time, through most or part of a day or even through many subsequent ones. Changing composition is especially noticeable during periods when many migrants are involved and also in situations where some flock members are territorial. As a result of differences in foraging speeds, individuals may be left behind. Despite frequent mention of such occurrences in the literature, some species commonly believed to drop out of such flocks regularly because of their slow rate of movement were seldom seen during my study away from mixed flocks. The Brown Creeper, for example, was observed away from flocks only once in 33 sightings while counts were made of flock participants in and out of mixed flocks on the three major Louisiana study areas (see Table XI). Such data may indicate that this alleged frequent dropout of

supposedly slower moving species is not always the rule. In Louisiana, dissociation probably occurs more frequently when a territorial member reaches the edge of its boundary; those not truly territorial often follow for longer distances.

Temperate flocks are seldom if ever permanent, gregariousness breaking down with the onset of reproductive behavior. Many tropical flocks are permanent or nearly so (Stresemann, 1917; Davis, 1946; Moynihan, 1962). Though individuals may drop out, the breeding seasons of the different members of the flock may be so staggered that they result in these groups being in permanent existence. Moreover, some actual nesting birds are sometimes found in the flocks (Willis, 1960; Moynihan, 1962). In his study on ant-tanagers, Willis suggested that flock permanence may be attributable to small clutch size, possession of a large territory, and presence of many nonbreeding individuals. Sooty-capped Bush-tanagers that I studied in Costa Rica usually had a clutch of two. Birds of this species in actual breeding condition spend part of their time in these flocks. Populations in the high Talamanca Cordillera during early April, 1964, the season of incubating, showed a notable tendency to confine their songs to early morning and evening and were much more apt to be found in flocks between these periods. Moynihan (1962) indicated that Common Bush-tanagers

studied on the Volcan de Chiriqui in nearby western Panama during their nonbreeding season showed indications of territorial defense early in the morning and late in the afternoon, though only for short periods of time.

In many flocks passive nuclear species are in a minority. Flocks that I studied in Louisiana did not contain more than one pair of Carolina Chickadees and one pair of Tufted Titmice. Often only one passive nuclear species is present, as in winter flocks of Black-capped Chickadees, Red-breasted Nuthatches, and Golden-crowned Kinglets that I studied in Maine. The reason is rather apparent. Passive nuclear species usually are not strongly attracted to other flock species, though the other species are strongly attracted to them.

In the flocks studied in Louisiana there are two species that may be considered passive nuclear, the Carolina Chickadee and Tufted Titmouse. Chickadees follow or join titmice more often than titmice follow or join chickadees. The White-breasted Nuthatch, Brown-headed Nuthatch, Golden-crowned Kinglet, and Pine Warbler might be considered active nuclear species in these groups. The Red-bellied Woodpecker, Yellow-bellied Sapsucker, Red-cockaded Woodpecker, Downy Woodpecker, Brown Creeper, Myrtle Warbler and a number of less frequent participants such as the Hairy Woodpecker, Carolina Wren, White-eyed Vireo, and Orange-crowned Warbler are considered

attendants. Of the species listed above, the Red-cockaded Woodpecker and the two species of nuthatches were studied mostly or entirely in the Longleaf Pine forest.

In the late summer-fall flocks in Maine, Black-capped Chickadees were passive nuclear species. Young Parula, Magnolia, Myrtle, Black-throated Green, and Blackburnian warblers also functioned effectively in this manner. Their begging calls strongly attracted other species of birds, including the Black-capped Chickadees upon occasion. The adult warblers of these species appeared to be attracted to the chickadees and other warblers. These adults might be classified best as attendants. Red-breasted Nuthatches, Golden-crowned Kinglets, and Black-and-White Warblers were common active nuclear species. Downy Woodpeckers, Brown Creepers, Winter Wrens, Bay-breasted Warblers, Yellowthroats, Canada Warblers, and American Redstarts, and several other less frequent species were also attendants.

The winter flocks in Maine contained many fewer species, the only regular members being Black-capped Chickadees, Red-breasted Nuthatches, and Golden-crowned Kinglets. Downy Woodpeckers and Brown Creepers were much less frequent. The roles of these five species in winter flocks are not significantly different from the ones that they hold in the late summer-fall flocks.

Several different flocks were studied for short periods in Costa Rica, and are listed according to their most prominent members: Blue Tanagers and Palm Tanagers; Common Bush-tanagers and woodcreepers; Sooty-capped Bush-tanagers; Scarlet-rumped Tanagers; and Tawny-crested Tanagers, furnariids, and woodcreepers.

SEASONAL FORMATION

Organized mixed flocks rotate closely about their passive nuclear members. In the North Temperate Zone, these flocks form after the breeding season, other members joining and following the passive nuclear members. In the flocks studied in Maine, though the Black-capped Chickadees are probably the chief passive nuclear species in the fall, a great amount of flock formation builds up around other sources. During my study, begging young warblers (Parula, Magnolia, Myrtle, Black-throated Green, and Blackburnian) made a great deal of sound that attracted other species, including the chickadees and Golden-crowned Kinglets. The young warblers followed their parents about the foraging areas that apparently contained the richest food supply on the island. Other species were attracted by the calls of these birds; thus the parents indirectly functioned as passive nuclear species.

Even a begging young Brown-headed Cowbird, parasitizing a Black-throated Green Warbler, proved to be a very strong attracting agent, primarily in all probability because of its very loud constant chatter.

Black-capped Chickadees were attracted to this species when it was begging. None of the attracted individuals exhibited any hostile reactions. The begging notes of this and one other young cowbird parasitizing a Black-throated Green Warbler in this area bore some resemblance to parulid begging notes.

The behavior of adult and young Black-capped Chickadees in late summer are quite different, the young first forming flocks (Odum, 1941b). At this time chasing and fighting become especially vigorous and may be the means of the establishing of a social hierarchy. In Massachusetts, Kluyver (1961) found adults and juveniles mingling in mixed flocks by mid-July, but he stated that family groups do not form the basis of a flock. Brewer (1961) noted that young Carolina Chickadees formed flocks before the adults and only later did the adults enter these flocks. Other species appear to form around pairs of Carolina Chickadees and Tufted Titmice in the flocks in Louisiana. In the fall there are sometimes extra birds (probably young) in these areas, particularly in the Longleaf Pine area studied. These individuals do not appear to be entirely tolerated and the commotion caused in defense of a territory may add to the attraction of a group for other species. This enforcement of territorial ownership may be similar to that effected by some English tits during a period in the fall (Gibb, 1956).

THE BREAKUP OF FLOCKS

A number of factors are responsible for the breakup of flocks. As indicated previously some tropical flocks may never break up.

Usually the major reason for the breakup of flocks is the appearance of reproductive behavior, heralded by an increase in song. Weather permitting, singing may begin in early January in the flocks in Louisiana, and as the season progresses it becomes more frequent. A notable increase of Tufted Titmouse song began on 4 January 1965, followed shortly by an increase in Carolina Chickadee song. At first, only occasional songs were given and these occurred in or near the flock. Later the members left the flocks for increasingly longer periods and moved about their territories independently, singing frequently. Often while alone they remained strangely silent if not singing.

When the passive nuclear species are involved in such activity, the eventual disruption of the flocks is signalled. Tufted Titmice are very prone to leave the flocks and cease calling, as do Carolina Chickadees to a somewhat lesser extent. The other flock members show

some tendency to continue following these individuals that withdraw; thus, breakup is usually a gradual affair. Odum (1941a) noted that flock breakup in Black-capped Chickadees is also gradual, while Hinde (1952) observed a similar breakup of English flocks containing Great Tits.

Early in the pre-nesting season reproductive behavior is considerably modified by the effect of weather, being most prevalent on warm days. However, by mid-January, even cold or stormy conditions appear insufficient to curtail completely these activities in the flocks studied in Louisiana. Gibb (1954, 1960) in his English tits found that all species investigated began to sing in January. In Ontario, Lawrence (1949) noted singing of Black-capped Chickadees as early as 1 January, followed the next day by chasing.

Increase in testis size was noted in Brown-headed Nuthatches in Louisiana as early as 11 January 1965, and excavations of nesting cavities by this species were observed on 25 January 1964 and 30 January 1965.

TERRITORY AND RANGE

A territory may be defined as any defended area (Noble, 1939). This definition distinguishes between a territory and a home range (defined later).

During the breeding season, territoriality is a familiar phenomenon, though it probably is less studied and less understood at other times of the year. In this paper I am concerned with territoriality outside the breeding season, especially with respect to the effects it may have on flocking.

During the nonbreeding period, territoriality may vary geographically, even within a single species. The variation may be a result of the environmental conditions existing within an area during a given period. In southeastern Louisiana, Carolina Chickadees and Tufted Titmice are strongly territorial at this time, with few if any exceptions. Whenever a bird of either species meets a member of another pair of the same species, loud protest notes are given: a buzz note and excited chick-a-dee-dee-dee for the chickadee and a loud rasping note for the titmouse. Occasional supplanting attacks or, more rarely, contact fights occur.

Other writers describe various types of territorial defense for these species outside the breeding season. Dixon (1955) states that the population of Tufted Titmice he studied at and about College Station, Texas, showed, at least at times, a strong tendency toward territoriality in the winter. Many descriptions of the social tendencies of Carolina Chickadees and Tufted Titmice in the literature are difficult to assess, particularly those in state treatises, as they only mention that these species are found in flocks and make no note concerning defense of a territory. However, the literature suggests that a greater intraspecific flocking tendency may exist at the northern end of the range of both species. Brewer (1961) clearly indicates that Carolina Chickadees form winter flocks in Illinois. Dixon's studies (1959) on the Carolina Chickadee at College Station indicated to him that the pair bond in this species was probably stronger than in the Black-capped Chickadee, a species that does not defend a territory in the winter.

Casual observations may create a mistaken impression with respect to flock membership. In the fall and winter, Carolina Chickadees and Tufted Titmice are not noticeably noisy, except when they meet other individuals of their own species. When they are not involved in a territorial dispute, they give relatively few calls that will particularly attract the observer's attention to them. When

they are loud and conspicuous, these species usually are situated at the edge of a territory, often quarreling with one or more pairs of the same species. As titmouse and chickadee territories often broadly or almost totally overlap each other, there frequently will be conflicts between both species occurring at the same time. Presence in one of these throngs is not an indication that the individuals all belong to one flock, as will be determined if a conflict is watched. At times, four or even six individuals (two or three pairs) of one or both species may be seen. Usually a concentration of associated species is attracted to this region of maximum activity. Such a situation may provide the opportunity for some of these associates to switch flocks and continue on with a new one when the conflict terminates. These species may thus cover a home range not unlike one they would traverse by traveling with a nonterritorial passive nuclear species, such as the Black-capped Chickadee.

Southern and Morley (1950) found that adult English Marsh Tits, normally territorial throughout the year, spend a disproportionately great amount of time on the edges of their territories where conflict with neighboring pairs occurs. My field observations indicate that a similar situation probably exists in the cases of Carolina Chickadees and Tufted Titmice.

If one produces sounds designed to attract small birds, the effects just described may be obscured. Feeding stations may also alter the natural conditions.

Hinde (1952) indicates that if the food supply and winter conditions permit, territories may be held through the winter in the genus Parus. If these conditions are not favorable, the individuals may stay near the territory in flocks and reoccupy them as early as possible. This finding would indicate that the general energy situation is more adequate in the southern areas than in the northern areas for Carolina Chickadees and Tufted Titmice. It remains to be seen how the behavior of the individuals in Louisiana would be modified under the stress of severe climatic conditions.

The literature indicates that territoriality is extensively practiced among tropical species; however, with territories covering a larger area, with a great variety of species and low densities of species, intraspecific defense may not be as critical as it is in areas where densities of a species are higher. Moynihan (1962) found indications that such strongly flocking species as Palm Tanagers and Sooty-capped Bush-tanagers were territorial, at least for part of the time in which they were participating in mixed flocks. Davis (1941) has brought out the point that when the density of a species is extremely low, actual territorial defense may seldom

occur intraspecifically. Territoriality does not appear to discourage flocking in species of low density. Some tropical flocks contain a conspicuous variety of species but low numbers of individuals of each species per flock, often no more than one or two. Flock participation may provide a convenient way to cover the fairly large territories and thus could be a logical consequence to the conditions described above.

Very little information is available to indicate whether the size of territories may change during the winter season. Some parids apparently exhibit territorial behavior in the fall when the population density is still high, thus perhaps effectively limiting their own numbers (Gibb, 1960). The strong territorial behavior exhibited in November by Carolina Chickadees and Tufted Titmice when food is probably near maximum abundance may accomplish a similar effect in Louisiana. Dixon (1949) indicated that in the permanently territorial, usually non-flocing Plain Titmouse, the size of territories remained constant throughout the year when both members of the pair survived. Several woodpeckers (Red-bellied, Hairy, Red-cockaded, and Downy) and the White-breasted Nuthatch are flock members but nevertheless are territorial. Presence of more than two individuals of one of these species in a flock may indicate a meeting on the edges of their territories.

The degree of intraspecific gregariousness within a taxonomic group is extremely wide. Even in the genus Parus, a considerable range of variation is shown, as reviewed by Hinde (1952). A few species such as the Plain Titmouse are extremely sedentary and remain on territory year round, the young generally pairing in late summer or fall and showing little tendency toward flocking. Marsh Tits are territorial throughout the year, but the young, which generally do not pair until a later time, often flock in the winter and wander over established territories, seldom being attacked or displayed against by the territorial adults, though being subordinate to them (Morley, 1953). Other forms at least temporarily give up their territories during the winter and remain in the same vicinity or near it, as is frequently the case with the Great Tit. This species migrates regularly from the northern fringe of its range and sporadically from other areas. These examples probably parallel the range of variation exhibited by the Black-capped and Carolina Chickadees in eastern North America.

Defense of winter territories has the advantage of decreasing the difficulty of claiming an area for the time when it will be utilized for breeding purposes (Hinde, 1952). It is impracticable or impossible for birds to hold them in some environmental situations.

If conditions are not excessively poor, the most advantageous possibility is sometimes to form flocks in the general area of the territory and remain thereby to assure that the territory may be quickly claimed in the spring. With conditions still more unfavorable, the most advantageous action may be to migrate. While Black-capped Chickadees do not maintain a territory outside the breeding season, Odum (1941a) found that the dominant birds in a flock were the ones most likely to nest in the area in which they had foraged during the winter.

The pattern of adherence to territoriality at this time of year indicates that it may be considered an extravagance. The benefits that are obtained from such behavior are largely ones that cannot be capitalized upon until the spring.

Many flocking birds that are not territorial in wintertime occupy what Fitch (1958) has called a home range, which he defines as an area regularly utilized though not defended by an animal. Most mixed flocks regularly cover a certain area, which has been referred to by other names such as a feeding territory (Butts, 1931), winter territory (Wallace, 1941), collective territory (Colquhoun, 1942), feeding range (Odum, 1942), and flock area (Hinde, 1952).

The size of this range depends upon the kind and numbers of species and the resources at hand. Swynnerton

(1915) indicates that in southeastern Africa the size of the area foraged by a flock is greater in less densely wooded country. Hinde (1952) found that tit ranges often overlap slightly, though not extensively. In Michigan, Batts' (1957) Black-capped Chickadee flocks increased the size of their range as the winter progressed. Batts' results prompted Brewer (1961) to suggest that food was an important factor in determining range size. Studying Black-capped Chickadees in Massachusetts, Wallace (1941) found that ranges varied in size, and that the size might differ still more drastically from year to year depending upon the conditions.

These statements indicate that home range size is modified by the relation of the environmental conditions to the population, a factor that also appears to be important in determining the presence of absence of territoriality in the genus Parus.

PREDATION

One of the advantages most often attributed to flocking in small birds is better protection from winged predators. Such an advantage is believed by some (Bates, 1864; Moynihan, 1962; and others) to be an important or paramount function of mixed flocks. The fact that a protective mechanism exists in many different flocks is easily observed. The point to be determined, if possible, is the present importance of this phenomenon.

Many of the members of mixed flocks possess alarm notes, which function both intraspecifically and interspecifically. These notes will result in some type of escape reaction such as a dive to cover (Hinde, 1952; Morley, 1953) in European titmice, scattering (Sharpe, 1905; Hindwood, 1937) in some African and Australian flocks, freezing (Odum, 1942) in Black-capped Chickadees, or a confusion chorus (Grinnell, 1903; Miller, 1922) in Common Bushtits. A confusion chorus is a series of call notes given by many birds at a time, obscuring the direction from which a single sound originates.

Flocks under attack would supposedly benefit when they moved from a confusion effect (Allee, 1938:137),

in which the grouping and flock behavior of the prey species would make it more difficult for a predator to obtain them. Allee's statement was based largely upon the work of Welty (1934) on Daphnia, using Goldfish (Carassius auratus) as the predator. Experimental proof in a flock of birds would be difficult to obtain.

Writers have stated that in some cases association with certain flock members may afford actual physical protection for the others. Association of this sort is reported by Marshall (1900) and Swynnerton (1907) in some African areas. Flocking species often occur there with some species of drongos that are notable hawk-chasers. The drongos feed heavily on flying insects such as their flock associates are constantly flushing.

Even though flock birds have protective responses to winged attack, it is questionable whether these responses do more than compensate for the great amount of noise produced by these groups, which surely must make them more conspicuous to potential predators.

While many have commented upon predation by winged raptors, the attention paid to the phenomenon may be largely attributable to the spectacular nature of attacks rather than to frequent observations. In three years of field work in three separate geographical areas, I have seen few examples of predation or attempted

predation on woodland birds, none of these being successful. Skutch (1940) reported that he had observed on an average no more than one instance of predation or attempted predation per six months of field work during a period of 10 years in Central America. Johnson (1954) in his study of flocks and ant aggregations on Barro Colorado Island in the Canal Zone did not consider winged predators a serious problem. In his study on Pygmy and Brown-headed Nuthatches, Norris (1958) saw only one attempt at predation (this by a Sharp-shinned Hawk). These few examples do not indicate that successful predation on flocks never occurs, but do suggest that perhaps the incidence is under some circumstances sufficiently low that we may well reinvestigate preformed ideas on its importance. Moynihan (1962) felt that the main advantage obtained by the flocks that he studied was predator protection. He worked mainly with flocks of the tropical forest edge, and perhaps in such groups this factor is of more importance.

Chapin (1932) found that some of the largest and most tightly grouped flocks that he observed in the Congo were residents of thick forests. Flocks were more frequent there than in more sparsely foliated savanna woodlands, though large flocks were occasionally found in these areas as well. The flocks in more open country could benefit from mutual warning, but any confusion

effect would probably be minimized since the members are usually scattered through the thin vegetation. Flocks of the deep forests are afforded more protection than birds of the more open country flocks. It appears that one has to go farther than predation to explain the constitution of such groups. Mixed flocks are also characteristic of the deep forests of the East Indian region (Stresemann, 1917), the Amazon (Bates, 1864), and other comparable tropical regions.

In Central America there are numerous species of hawks, but they are generally not common and many do not prey on small birds (Skutch, 1940).

In many parts of the North, few if any diurnal avian predators of small birds are present in the winter, though this season is the one at which flocks are the most highly developed. The scarcity of such a type of predator is especially noticeable in heavily wooded areas, where the sporadic Gray Shrike is infrequent. Sharp-shinned Hawks and Cooper's Hawks, the major bird hawks in these areas, do not regularly remain this far north during the winter season.

While response to a group alarm call may improve chances for successful escape, the action does not always work perfectly. There are observations of the European Sparrow Hawk preying specifically on flocks in spite of their alarm mechanism (see Morley, 1953).

When the energy involved in food finding is considered, predator attacks upon mixed flocks may not be more expensive than the extra energy involved in hunting for and finding solitary individuals. The energy demand would be especially great if some of the single individuals were territorial birds, which, though not as effectively apprized of danger as they would be in a flock, probably do know their area better than the flock knows its home range. Dixon (1949) felt that Plain Titmice he studied in California obtained considerable predator protection by remaining on territory in pairs. His contention was that the pairing confers much of the protective advantage obtained by presence with many other birds in a flock.

I made scattered observations of predator reactions in the pines at Fluker. Three or more American Sparrow Hawks wintered in the study area and were not infrequently seen. Although none was observed actively attacking the flocks, and eliciting an alarm response. This response was usually commenced by Carolina Chickadees rather than the primary leaders of the flock, the Tufted Titmice. The chickadees would sound the alarm, an unusually sibillant chick-a-dee note, often ending in several very high dee-dee-dee notes. Sibillant notes are more difficult to locate than ones of lower frequency, and are therefore of additional survival benefit (see

Thorpe, 1961:32). As they gave the alarm call, the chickadees dived into the understory, where they frequently continued the sibillant notes. Other members of the flock reacted in various ways and in varying degrees. I observed that chickadees gave the initial response rather than the primary leaders of the flock, the Tufted Titmice. Titmice reacted much less definitely, having a less pronounced tendency to move into the thick understory and at times remaining nearly motionless at the point where they were foraging. At least twice, titmice were seen flying vulnerably in the open directly after a pass by the hawk and before the chickadees began to resume normal activities. These birds were not attacked, but such a maneuver would definitely subject them to predation. Pine Warblers appeared to curtail their activities, though remaining in the pines. Brown-headed Nuthatches decreased their foraging noticeably during these periods, though not completely ceasing them. At one time when a Sparrow Hawk flew over a pure flock of nuthatches, these birds gave rather loud alarm notes, which closely resembled their normal loud <u>see</u>-<u>see</u>-<u>see</u> notes. These alarm notes caused activity to diminish considerably, though it did not completely cease. Red-cockaded Woodpeckers appeared to ignore alarm notes completely, calling regularly and continuing their activities after the warning notes had been given.

Winterbottom (1943) noted in Northern Rhodesia that Cardinal Woodpeckers did not respond to call notes. He further stated that there was little interspecific communication of alarm signals in these flocks.

Small groups consisting of Eastern Bluebirds, Slate-colored Juncos, and Chipping Sparrows occasionally moved along with the mixed flocks in the Louisiana pinelands. The juncos and sparrows usually foraged on the ground, while the bluebirds frequently flew down to it from low limbs in order to pick up objects of food. The ground probably was the most vulnerable stratum, because of the sparse undergrowth in most of these areas. These birds responded strongly to Carolina Chickadee alarm notes, usually scattering simultaneously and lighting in the lower limbs of the pines. These birds, particularly the two fringillids, have feeding habits very different from those of the woodland flock species, whose members only occasionally work on the ground, and then perhaps not for the same food items. Because of their vulnerability on nearly open ground, the bluebirds, juncos, and sparrows possibly benefitted more from the predator alarm than did any of the customary flock members.

Activity returned toward normal after such alarms as soon as the Carolina Chickadees began calling again with their normal chick-a-dee notes, and began to hop about in the low vegetation where they had sought cover.

Myrtle Warblers and Ruby-crowned Kinglets were seen to emerge from low vegetation following alarm calls on different occasions, and it is likely that they seek cover at this level, though they are frequently found foraging in the more exposed parts of this underbrush.

By their very foraging positions, some of the just mentioned species are more vulnerable to predation than others. In the pinelands, those species most often found in the defoliated deciduous understory are those showing a greater response to predator alarm notes. The species usually giving these notes, the Carolina Chickadee, forages extensively in this part of the stratum. Less response is shown by species occupying a less vulnerable position in the pine trees.

In summation, these responses are of some survival benefit, particularly to the Carolina Chickadees and to the occasional ground-feeding birds attaching themselves to such a flock. However, in view of the reactions of some of the species, including the Tufted Titmouse, to the alarm notes it is unproved that it would be more advantageous for a predator to hunt nonflocking birds. It is difficult to hypothesize that flocking conveys a significant predator protection benefit for all species; otherwise, a more definite response might be expected.

Frequently, false alarms are given. My observations on 31 July 1962 at Hog Island, Maine, illustrate a typical case. A flock of several species of warblers were foraging in the crown of a White Birch when a Black-billed Cuckoo suddenly and silently lit in their midst. A high-pitched alarm note was given and the warblers immediately dived for cover. After a short time, they congregated in a nearby White Birch and continued foraging. After a few minutes the cuckoo lit in this tree, causing repetition of the same reaction. It appeared to be feeding on a heavy infestation of microlepidopteran larvae and remained foraging after the warblers had departed.

In the Satsuma, Louisiana, study area, Mourning Doves that flew at a low level over trees containing Carolina Chickadees sometimes elicited a predator alarm response. No flocks studied in Louisiana reacted to Turkey Vultures or Black Vultures flying overhead. However, none of the vultures observed ever flew at a height less than 100 feet over the trees.

Hinde (1952), Morley (1953), and Gibb (1960) observed English tit flocks giving alarm responses to Wood Pigeons, and Hinde further mentioned that Blackbirds at times caused such a reaction. Scrub Jays have been known to cause Common Bushtits to produce this response (Miller, 1921).

Mixed flocks on Hog Island did not respond to Double-crested Cormorants, Great Blue Herons, Great Black-backed Gulls, or Herring Gulls when these species flew over the trees at a low level. Neither did these flocks respond to Blue Jays; however, the jays were very noisy and moved rather deliberately, seldom making a silent abrupt move.

If false alarms occur relatively often, they may cause useless expenditure of too much energy to be of selective advantage, especially if foraging time and energy relationships are critical.

In spite of the fact that the above argument does not heavily support predator protection as an important function of flocking, the fact remains that predator alarms do persist. Hence, an attempt to explain why such an alarm system does exist is in order at this point.

There are two extremes possible, flocking and a solitary existence, each having its advantages. Even if territoriality or random solitary wandering represented a more efficient defense against predation than flocking, flocks could develop if flocking bestowed other more important advantages upon the individuals that began this practice. Evidence is supplied elsewhere in this paper that other advantages are obtained through flock participation.

If there are two flocks, one with a tendency toward some defense mechanism and the other without it, the individuals in the flock with this mechanism will tend to have a higher survival rate than birds in a flock without it, if predation is of any importance. Flock predator alarms could arise out of such a situation without predator protection being the principal benefit of flocking. Thus, predator alarms may aid in permitting flocking rather than being the basic advantage of flocking itself.

Predation on the individuals that occurred in mixed flocks may be more selective than that upon territorial individuals. When several individuals are present, a choice exists for the predator. Thus, predation upon the less alert individuals would become more pronounced, and the predator would spend less time attempting to capture the most fit individuals than it would when randomly attacking single territorial birds, which do not present such a choice.

The mobbing reaction is another response related to predator defense, and one that is well developed in some mixed flocks. The response is given under different circumstances than the winged predator alarm; it usually is directed toward perched avian predators (Hinde, 1952) and sometimes to potential non-avian predators. A perched hawk will be mobbed, but when it

flies, the winged predator response will occur. The seeming function of mobbing is to announce the position and presence of the predator, making it impossible for it to utilize the element of surprise in procuring prey (Nice and Ter Pelkwyk, 1941).

AGGRESSIVE BEHAVIOR

Conspicuous plumage, song, and territoriality are three conditions eliciting hostile behavior in potentially flocking species.

Hostile actions (supplanting "attacks", fights, and chases) provoke responses quite different from "friendly" actions (joining and following). The effect of the former is usually to break up flock organization; that of the latter to enhance them. On a few occasions, supplanting "attacks" are perhaps accidental, as when one species replaces a second that is not a close competitor. A Red-bellied Woodpecker that I observed alight on a trunk immediately adjacent to twigs where a Ruby-crowned Kinglet was foraging, causing it to fly off, furnished an example of such a relationship. Unsuccessful supplanting "attacks" may sometimes take on the appearance of joining actions.

The more highly organized members of a flock will spend a minimum of time performing aggressive behavioral displays against other species. Those expressions of aggressiveness that do occur may be limited largely to supplanting "attacks". Carolina Chickadees and Tufted

Titmice serve as excellent examples, very few attacks (except for occasional supplanting "attacks") being launched upon one by the other. What overt aggressive behavior occurs is one-sided, the titmouse being dominant over the chickadee in this respect. The interspecific peck order in English flocks was found to be largely dependent upon the body size of the individuals concerned (Colquhoun, 1942; Morley, 1953). This principle appears to operate in flocks in Maine and Louisiana also.

Carolina Chickadees and Tufted Titmice possess well developed aggressive notes that appear to attract other species, and which are distinct from their conventional songs. Moynihan (1962) noted a similar interspecific effect resulting from the hostile notes of Common Bushtanagers.

In comparison to some of Moynihan's flocking species, the temperate passive nuclear species tended to perform fewer aggressive actions against other flock members. Tufted Titmice and Carolina and Black-capped Chickadees were notable in this respect. One factor that might reduce the frequency of aggressive acts is that more ecological overlap usually occurs among flocks that contain many quite similar species. Though Carolina Chickadees and Tufted Titmice are both placed in the genus Parus, the difference between the two in size and bill shape suggests an ecological difference (see Table IV)

that is probably considerably greater than that between some congeneric tanagers found in a single flock.

Where the more organized flock members are not territorial, as in the Black-capped Chickadee, a social hierarchy develops (Hamerstron, 1942; Odum, 1942) and after its establishment in the fall, a relatively small amount of energy is expended in intraspecific aggressive behavior. The largest flocks appear to show proportionately more hostile behavior than smaller ones.

A common hypothesis is that the more closely related that species are to each other, the greater the competition between them, unless special adaptations have been developed that reduce this effect. However, Moreau (1948) found that where more than one species per genus or family was present in a flock, in most cases the foraging habits were complementary. Gibb (1960), in his study of Goldcrest and mixed tit flocks, found differences in foraging behavior between the species, though it was sometimes slight. He felt that the species in the flock must limit the density of each other, since they often fed heavily upon the same species of prey.

Where complementary behavior does not occur, considerable hostile behavior may be expended if the species involved are in the same flock. The rather closely similar Golden-crowned and Ruby-crowned Kinglets are usually somewhat separated by habitat preferences and

foraging height during the critical winter season and also are usually only narrowly sympatric at this time. The Golden-crowned Kinglet periodically stages southward incursions, and then the habitat separation often breaks down. No Golden-crowns were definitely seen in the Louisiana study areas during the 1963-64 winter; however, they were fairly common through most of the 1964-65 period. In Kansas, Fitch (1958) found that during the winter the Golden-crowned Kinglet frequented brush and other typical Ruby-crowned Kinglet habitat. The Ruby-crowned Kinglet was not noted there at that time of year. In mixed pine-deciduous habitats in Louisiana, the Golden-crowned Kinglet foraged in pine considerably more than the Ruby-crowned Kinglet and usually occurred higher in the vegetation (see Tables I and II). In largely deciduous areas, the Golden-crowned Kinglet also foraged higher than the Ruby-crowned most of the time, often working in foliage of the mid and upper stories in comparison to the Ruby-crowned, which usually worked the understory foliage and brush. However, Golden-crowned Kinglets were not infrequently found in the understory. The two species foraged quite similarly, gleaning in the foliage and branch tips and often hovering. Frequent displays of hostility were seen between the two species, often involving wing-flicking and erection of the brightly colored crown feathers. Such

encounters nearly always occurred in the understory, where the instigator and accustomed resident, the somewhat larger Ruby-crowned Kinglet, always seemed successful. Occasional encounters at higher levels were seen, the Ruby-crowned Kinglet again being the aggressor and also always appearing successful here. Flock estimates indicated the possibility that the Ruby-crowns were limiting the numbers of Golden-crowns in flocks (see Table III). This phenomenon was most noticeable in the Longleaf Pine area, the plot in which most of the hostile behavior was exhibited. This area supported fewer birds than the other areas (see Table VIII), and hostile behavior may be most pronounced under such circumstances. A limited number of observations in the deciduous forest study area also indicated a greater tendency for hostile encounters to occur there than in the mixed pine-deciduous habitat. The results suggest that the more limited forage choices in the two pure habitats (pine and deciduous) may act to inhibit mutual participation in flocks. There also was a greater tendency for Golden-crowned Kinglets to be found foraging in the lower 30 feet of the forest in the mixed pine-deciduous area than in any other area. Because of the similarity in appearance and behavior of these two species, accurate flock counts for them were difficult to obtain, though the figures obtained probably indicate the actual ratio fairly well.

TABLE I

FREQUENCIES (IN PERCENTAGES) ACCORDING TO FORAGING HEIGHT OF GOLDEN-CROWNED AND RUBY-CROWNED KINGLETS IN MIXED-SPECIES FLOCKS IN LOUISIANA DURING THE WINTER OF 1964-65[1]

Forage height	Deciduous[2]		Pine-deciduous[3]		Pine[4]	
	Golden-crowned	Ruby-crowned	Golden-crowned	Ruby-crowned	Golden-crowned	Ruby-crowned
Above 30 feet	35.0 (7)	0.0 (0)	48.6 (27)	0.0 (0)	22.8 (6)	0.0 (0)
30 feet or below	65.0 (13)	100.0 (14)	51.4 (29)	100.0 (41)	71.2 (20)	100.0 (48)

[1]The number of birds is enclosed in parentheses.
[2]Baton Rouge study area.
[3]Satsuma study area.
[4]Fluker study area. Includes oak understory.

TABLE II

FREQUENCIES (IN PERCENTAGES) ACCORDING TO FORAGING PREFERENCES OF GOLDEN-CROWNED AND RUBY-CROWNED KINGLETS IN MIXED-SPECIES FLOCKS IN LOUISIANA DURING THE WINTER OF 1964-65[1]

Forage preference	Pine-deciduous[2]		Pine[3]	
	Golden-crowned	Ruby-crowned	Golden-crowned	Ruby-crowned
Pine	28.8 (16)	4.8 (2)	84.8 (22)	14.7 (7)
Deciduous	71.2 (40)	95.2 (39)	15.2 (4)	85.3 (41)

[1]The number of birds is enclosed in parentheses.
[2]Satsuma study area.
[3]Fluker study area. Includes oak understory.

TABLE III

NUMBERS OF GOLDEN-CROWNED AND RUBY-CROWNED KINGLETS IN MIXED-SPECIES FLOCKS IN LOUISIANA DURING OCTOBER AND NOVEMBER, 1964

Area	Date	Number of Golden-crowned	Number of Ruby-crowned	Number of birds in flock
Deciduous[1]	November 27	1	2	16
		5	1	24
Pine-deciduous[2]	October 28	4	4	17
		2	2	9
	November 8	0	1	8
		2	0	9
	November 18	5	4	26
		3	2	22
		0	1	8
	November 26	1	2	19
		4	0	18
		1	0	6
Pine[3]	November 6	1	0	26
		0	1	18
		1	2	16
	November 11	1	5	47
		5	1	32
		1	4	33
	November 21	2	4	92
	November 29	1	0	14
		1	0	32
		1	1	25
		0	2	22

[1]Baton Rouge study area.
[2]Satsuma study area.
[3]Fluker study area. Includes oak understory.

After fall movement ceased, Ruby-crowns seldom were intraspecifically gregarious and appeared to hold winter territories. Thus, not enough individuals of this species would be found in a flock to check further whether Ruby-crowned Kinglets were limiting Golden-crowned Kinglets in flocks. Occasional displays of hostile behavior by Ruby-crowns toward Golden-crowns were still seen.

Relatively little published information exists that indicates whether considerable hostile behavior exists during periods of great food abundance. Hostile behavior does not disappear under such circumstances in the flocks that I have studied. The normal behavioral patterns apparently are not easily or quickly changed. Indications are that the presence of an abundant food source may actually increase hostile behavior at times, probably as a result of the change of foraging patterns to a degree that more overlap and contact occur among some of the species. The Longleaf Pine seed crop during the 1964-65 winter caused a modification of foraging patterns, including the necessity of visiting cones and finding a suitable place to crack the seeds. Several instances of hostile behavior between Pine Warblers and Brown-headed Nuthatches and somewhat fewer examples between Carolina Chickadees and the two other species were recorded.

Most of the species displaying a high frequency of hostile behavior in temperate flocks are the temporary members in the late summer and fall, especially several warblers that winter south of the United States. The Myrtle and Pine Warblers winter widely through the southern United States; but they are exceptions, and some of their adaptations may explain their presence. Both are capable of supplementing their diet with vegetable matter; Myrtle Warblers eat berries of the Wax-myrtle (Myrica cerifera) and in the Louisiana study areas Pine Warblers eat pine seeds. The Myrtle Warbler is a species highly gregarious intraspecifically and has a tendency toward nomadism. The Pine Warbler is adept at foraging on heavy bark as well as in the foliage.

A high degree of hostile behavior and a marked tendency to gather in large numbers probably are factors that reduce the advantages to Myrtle Warblers of association with a mixed flock. The greater tendency for this species to break away from mixed flocks, especially when in large numbers, may reflect the lesser advantage of mixed flock participation for them.

A large percentage of the elaborate interspecific conflicts of the winter members of late summer-fall flocks in Maine appear to be with the temporary fall members and are usually instituted by the fall members. Autumn is a period of abundant food, but the overlap of

feeding niches in these species is considerable, probably heightening such behavior. Few occasions were noted in which both participants were members of the winter flocks, and these were simple supplanting attacks.

Territorial birds are more widely spaced than flock members. In addition, flocking conflicts are different from territorial defense in that no concrete plot of ground is defended, but rather a certain space around the individuals, continually changing as they move about their habitat.

The distance that individuals are spaced is the product of opposite drives of mutual attraction and mutual repulsion (Emlen, 1952), and is modified by the foraging conditions existing in the habitat. The tolerable distance will vary depending upon whether the individual encountered by a bird is of the same species, a close competitor, or one not competing strongly. While most species exhibit less hostile behavior interspecifically than intraspecifically, exceptions occur in the flocks, such as the relationship existing between Golden-crowned and Ruby-crowned Kinglets.

This distance varied considerably in the mixed species flocks studied. Though mixed insectivorous flock members were bunched together much more closely than strictly territorial species, there seems little question

that they seldom were found extremely close to each other. Most species did not allow approach by another individual closer than one to two feet without displaying some sort of hostile behavior or escape reaction. Seldom did individuals remain closer than five feet to each other. The Brown-headed Nuthatch permitted much closer approach, particularly by other individuals of its own species. Upon several occasions two individuals were seen foraging without apparent concern upon the same cluster of Longleaf Pine cones, occasionally even touching each other. Some of the members of the tropical tanager and honeycreeper flocks studied by Moynihan (1962) permitted extremely close approach of other individuals upon occasion. My personal observations in Costa Rica indicated that Blue Tanagers often allowed a closer approach by other individuals of their own species than did most temperate flock members that I studied.

Location notes of the Ruby-crowned Kinglet and Audubon's Warbler were hypothesized by Grinnell (1920) to function in keeping the birds spaced on their wintering grounds, thus preventing the same small area such as a tree or bush from being foraged upon more than once. He considered these species essentially nonflocking. McAttee (1920) pointed out that this explanation is generally untenable. In addition, my field studies in Louisiana did not bear out Grinnell's

thesis. Any area was foraged in several times during the passage of a large flock of the closely related Myrtle Warblers. Myrtle Warblers were often found in such large numbers that location notes would appear to be of little use in preventing reforaging of an area. Myrtle Warblers do occasionally defend winter territories (see Woolfenden, 1962), but such behavior was not observed in study areas in Louisiana. Ruby-crowned Kinglets were often found in numbers ranging up to eight prior to apparent establishment of a winter territory in December. After a territory was established, the notes in question would not be of use in spacing.

FORAGING

Members of the flocks I studied in Maine and Louisiana are typically insectivorous. There is no indication that any of these birds are completely independent of insect food over a considerable period of time. Many of the mixed tropical flocks are largely insectivorous, though those studied by Moynihan (1962) contained a large number of frugivorous and nectarivorous forms in addition to insect feeders. However, a great feeding overlap occurs. Skutch (1954) states that seldom if ever do any of the tanagers subsist on a diet excluding insects. It is possible that the members of these flocks possess a widely scattered but overlapping set of food preferences, and that while the species at opposite ends may not overlap in this respect, they may be part of a widely interlocking system. Though more species are found in tropical habitats than in comparable temperate ones, more opportunities for species diversity also exist (see Fischer, 1960) or because of increased niche overlap (Klopfer and MacArthur, 1961). Thus the foraging competition facing tropical species

may be comparable to that found in the temperate zone. As the foraging patterns of some of the temperate flock members are almost exclusive (e. g., Brown Creeper and Golden-crowned Kinglet) though only the opposite ends of an interlocking chain, it is not unreasonable to believe that an analogous situation may exist in other cases, including tropical ones.

Birds utilize a number of different ways of obtaining insect food, including probing, gleaning, flycatching, hovering, and drilling. Chickadees regularly glean, hammer, and pry; titmice hammer and pry; nuthatches probe and perform limited excavations, getting into deeper openings than the parids; creepers probe and pry into the deepest crevices; kinglets glean; Pine Warblers may survey bark and crevices, glean, and flycatch; woodpeckers excavate. Flocks contain several of these species and therefore utilize a great variety of foraging methods.

In addition to the separation by means of differences in foraging procedure, flock members may be separated by preferences regarding foraging height, tree species, and tree parts (Hartley, 1953). These differences need only be statistical to be of significance. Such correlations have been found in English mixed tit flocks by Hartley and others. My data show a definite evidence that different heights and tree parts are

frequented by different species. Feeding behavior may vary radically during the course of a year. The data of Norris (1958) and my own findings indicate that such variation exists with regard to Carolina Chickadees, Tufted Titmice, Brown-headed Nuthatches, and some other birds of the Longleaf Pine forests. During the winter season all these species feed very heavily upon pine seeds when they are available. At other times they are principally insectivorous. Varying preferences for tree species exist also. In mixed pine-deciduous and pure deciduous forests, Tufted Titmice feed heavily upon acorns where they are available, and a definite preference for oak trees may be noted. Carolina Chickadees and Tufted Titmice spend a great amount of time along stream edges in the Longleaf Pine forests, probably because of the greater abundance of deciduous arboreal growth found there. In these forests Ruby-crowned Kinglets frequent deciduous growth almost exclusively.

External morphology, especially as seen in the bills of different species, often gives a valuable clue to the methods of feeding utilized, though it does not always elucidate the entire situation. The Brown-headed Nuthatch has a long bill, quite typical of the family Sittidae and ideally suited for probing. Yet it feeds on pine seeds heavily in some winters. The seeds of the Longleaf Pine are regularly obtained by even Carolina

Chickadees and Tufted Titmice, so the long bill is not necessary for this type of foraging. The condition of the ventriculus may provide a further clue to the total feeding pattern of the Brown-headed Nuthatch. This structure is large with heavy muscular walls, probably an adaptation for satisfactorily processing the pine seeds. The Pygmy Nuthatch, which is even more highly vegetarian than the Brown-headed Nuthatch, has a still larger stomach, which Norris (1958) tenatively related to the greater amount of vegetable food taken. A thin-walled ventriculus might not satisfactorily process a seed diet; on the other hand, a powerful stomach could process insects. This capability is important outside of the seed season and in the years of poor crops of pine seed. The ability to feed on insects thus is a necessity, even though pine seeds will be used when available in sufficient quantities. A point of interest is that the Brown-headed Nuthatch has probably become adapted to a food supply that is not completely dependable. Burleigh (in. litt.) stated that in Mississippi there was a tendency for movements into nearby stands of other pine species when the seed supply of one was poor. I noticed little or no sign of emigratory or immigratory movements by the flocks that I studied in the extensive Longleaf Pine woodlands even though the seed crop was light in the 1963-64 winter and heavy in

the 1964-65 winter. The average density in a sample study plot there in the 1964-65 winter was 17.2 birds per 100 acres (see Table VIII), within the normal range of variation of Brown-headed Nuthatch populations compiled by Norris (1958). Little difference from the frequency and occurrence of the species in the previous winter was noted. Perhaps the extensive size of the pineland plus the relatively sedentary character of this species may have accounted for the lack of such an effect as Burleigh describes.

When more than one rather closely similar species is found in a habitat, some adaptation probably is present that facilitates their foraging together. Any one or more of the previously mentioned conditions may make this possible. Gibb (1954) found in English mixed tit flocks that distinct, if sometimes slight, differences in foraging habits existed among the species when there was not a superabundant food supply. A superabundant supply tends to obliterate these differences. In the absence of such a condition, the amount of permissable overlap is dependent upon other factors such as the number of competing species, the resources of the habitat, and energy demands of the species. To a considerable degree, the feeding behavior of an individual, especially one of a less dominant and less aggressive species, may be determined by the other species present.

In northern flocks, such as in Maine during the winter, few species are present and there is little overlap. These circumstances may be an indication of a less satisfactory habitat.

Where regularly found together in flocks, species may be expected to present enough differences to make presence of more than one of them possible. In spite of the differences antagonistic behavior is not lacking; in fact, with closely similar species involved there will be considerable conflict. If such a condition is developed and a change in the habitat occurs, as by the presence of a superabundant food source, foraging behavior may become modified somewhat. Hostile behavior may still occur. However, if hostility is not excessive, the increased food supply obtained may be more than sufficient to offset time and energy lost to aggressive actions.

In the late summer-fall flocks in Maine, there are many more species than in the winter flocks, some with quite similar foraging patterns and possessing much more hostile behavior in the flocks than the permanent residents. Conditions are not so critical and at this time a much more adequate food source is present.

Selective pressure works toward survival of a group of characters in different species that permit maximum utilization of the habitat, something that could not

be attained by one species. A species that is broadly generalized in a rich environment will face considerable pressure from other species and cannot maintain its varied foraging procedures unless it can compete under a variety of conditions. The Black-and-White Warbler is perhaps the most diversified forager studied intensively in any of my study areas. In addition to climbing on trunks and limbs with nearly the ability of a nuthatch, it frequently gleans the foliage of flycatches; on occasion it even hovers or hangs. Such a pattern results in its frequent meetings with a great many other species. The Black-and-White Warbler is an extremely aggressive species. Its behavior, plus a size somewhat superior to that of most competing species, usually permits it to be successful in its numerous encounters, most of which it instigates.

Most of the flocking species are much more specialized and thus do not encounter as many other species regularly in their normal foraging pattern. The more specialized species include the Brown Creeper, which is found almost exclusively on tree trunks, and most commonly only the lower parts of the trunks. The creeper is not aggressive and in its habitat has less contact with other species than most or all of the other flock members. In addition, it is small and is seldom successful in any hostilities with other flock members.

Winter flocks in Maine contained fewer species on an average than late summer-fall flocks in Maine and in Louisiana. This factor favors species that are more generalized and have larger niches than in areas where more species occur. Perhaps this paucity of species results in a simpler equilibrium. The winter flocks never consisted of more than three species and generally contained fewer individuals than the other flocks studied. Species included Black-capped Chickadees, Red-breasted Nuthatches, and Golden-crowned Kinglets, which split up the available habitat. Birds of the other insectivorous flocking species were quite uncommon here and included Downy Woodpeckers and Brown Creepers. Most flocks did contain all three main species, the chickadees usually foraging widely on the limbs from the outer parts toward the trunk, the Red-breasted Nuthatches generally working the trunks or the part of the large limbs nearest the trunk, and the Golden-crowned Kinglets feeding mostly in the twigs. The Black-capped Chickadees hung occasionally, though less frequently, on the outermost tips of foliage, and thus the kinglet's utilization of the outermost fringe of the vegetation was subject to less interference than in Louisiana. Field work in Louisiana also indicated that Carolina Chickadees hang more frequently than Black-capped Chickadees do. In addition, the Golden-crowned Kinglets frequently

hover at the tips of twigs and foliage and thereby glean in a sport that is otherwise inaccessible. These two adaptations give the Golden-crowned Kinglet and both chickadees access to a food source otherwise unavailable except where parts of it can be reached by stretching from surrounding vegetation. Hovering and hanging are not identical in the benefits bestowed: a hovering bird can glean anywhere, even at the branch tips, but it cannot effectively peck or excavate. The chickadees can peck and excavate, but they are somewhat restricted in the places where they can hang; thus, they cannot readily reach some spots, especially on larger needles or on leaves.

In Maine, Golden-crowned Kinglets showed a greater tendency than Black-capped Chickadees to work in coniferous growth throughout the year. Black-capped Chickadees definitely led flocks in which both species were found, and in a rather limited number of observations in December, the kinglets showed some tendency to work lower than the Black-capped Chickadees and lower than when in pure flocks. Golden-crowned Kinglets are most often seen upon the ground when with chickadees. In mixed habitats, distinctions in foraging heights are less marked, because of the coniferous preference of the kinglet and the greater tendency for the chickadees to feed in deciduous growth.

I have observed other species attempting foraging gymnastics with varying success. I have seen Golden-crowned Kinglets at times hang from a branch tip, but with considerable difficulty and with questionable success. Some of the late summer-fall warblers frequently hover, stretch, or flycatch. Among the warblers studied the Black-throated Green is the most persistent and probably the most successful hoverer, though hovering is performed upon occasion by a number of other species, including Blackburnian, Magnolia, and Myrtle Warblers. Most of the warblers in these flocks flycatch, but the Myrtle does so most commonly. The proportionate frequency of these feeding adaptations being utilized in some of the species is closely similar to that found for the same species during the breeding season by MacArthur (1958).

In the Louisiana flocks, Ruby-crowned Kinglets are as adept at hovering as Golden-crowned Kinglets are and perhaps resort to this practice even more frequently. Both Carolina Chickadees and Tufted Titmice can hang, but the chickadee utilizes this foraging procedure much more frequently than the titmouse. The titmouse usually works in this manner while obtaining vegetable food, especially hackberries. This is a food source not regularly used by the chickadees.

Black-capped Chickadees in Maine appeared to occupy essentially the same parts of the habitat as the Carolina Chickadees and Tufted Titmice combined in Louisiana. It is of interest that the Black-capped Chickadee is intermediate in size between the other two species, though much closer to the Carolina Chickadee.

Brewer (1963) supplied foraging data for Black-capped and Carolina Chickadees in Illinois. My Carolina Chickadee data from Louisiana (Table IV) are consistent with his, though my Black-capped Chickadee figures from Maine (Table V) deviate widely. The difference between the foraging positions of the Black-capped Chickadee in Maine and Illinois may be due partly to the presence of Tufted Titmice in the latter area and their absence in Maine. Table V clearly indicates a complementary foraging relationship between Carolina Chickadees and Tufted Titmice in Louisiana, more prevalent in some habitats than others but very marked in all areas studied. Though varying somewhat in detail, Brewer's figures clearly show that in Illinois the patterns of the two chickadees differ only in small details. My Black-capped Chickadee data indicate that in Maine this species regularly utilizes a greater part of the habitat than in Illinois. The Black-capped Chickadee is the only regular member of the genus Parus found in southern Maine. Thus, it does not face competition with the

TABLE IV

FREQUENCIES (IN PERCENTAGES) ACCORDING TO FORAGING PLACEMENT OF CAROLINA CHICKADEES AND TUFTED TITMICE IN MIXED-SPECIES FLOCKS IN LOUISIANA FROM OCTOBER TO MARCH[1,2]

Foraging Position	Carolina Chickadee			Tufted Titmouse		
	Deciduous[3]	Pine-deciduous[4]	Pine[5]	Deciduous	Pine-deciduous	Pine
Ground and herb	0.0 (0)	0.0 (0)	5.7 (11)	0.0 (0)	0.0 (0)	0.0 (0)
Shrub and thicket	19.7 (11)	9.9 (14)	7.7 (15)	23.5 (12)	9.7 (11)	1.2 (2)
Vine	7.1 (4)	1.4 (2)	0.0 (0)	9.8 (5)	3.5 (4)	0.0 (0)
Small branches[6]	50.0 (28)	73.1(103)	56.2(109)	27.5 (14)	26.6 (30)	36.5 (61)
Large branches	23.3 (13)	11.3 (16)	29.4 (57)	35.3 (18)	54.0 (61)	57.5 (96)
Bole	0.0 (0)	4.3 (6)	1.0 (2)	3.9 (2)	6.2 (7)	4.8 (8)
Totals	56	141	194	51	113	167

[1]Years 1963-64, 1964-65
[2]The number of birds is enclosed in parentheses.
[3]Baton Rouge study area.
[4]Satsuma study area.
[5]Fluker study area. Includes oak understory.
[6]Includes fruits, cones, and foliage.

TABLE V

FREQUENCIES (IN PERCENTAGES) ACCORDING TO FORAGING PLACEMENT OF BLACK-CAPPED CHICKADEES IN MIXED-SPECIES FLOCKS IN MAINE[1]

Foraging Position	July-September[2]	December[3]
Ground and herb	0.6 (1)	0.0 (0)
Shrub and thicket	3.1 (5)	0.0 (0)
Vine	0.0 (0)	0.0 (0)
Small branches[4]	45.7 (74)	40.9 (18)
Large branches	48.8 (79)	54.5 (24)
Bole	1.8 (3)	4.6 (2)
Total	162	44

[1]The number of birds is enclosed in parentheses.
[2]Hog Island study area, 1962-64.
[3]Androscoggin County, 1964.
[4]Includes fruits, cones, and foliage.

Tufted Titmouse, a species present in all the other areas studied by Brewer and myself. The frequent or usual association of titmice and chickadees in mixed flocks probably serves to enhance a complementary foraging relationship. In Maine, there was considerable variation in the foraging patterns of the Black-capped Chickadee. In the late summer-fall flocks found in the White Birch-spruce study area, the foraging appeared dependent upon the abundance of insects attacking the birch foliage. When heavy, as in the 1963 season, the foraging pattern of this species would approach that shown by Brewer for Illinois birds. When the insect infestation was low, as in 1964, a pattern almost the reverse of that of the previous year was found, the birds working heavily on the bark and lichens (mostly Usnea sp. and Parmelia sp.) of the larger limbs. Thus, this species displayed an ability to alter its foraging pattern widely, probably more widely than would be possible if it faced congeneric competition. Limited winter observations indicated that this species is even more apt to be found on large limbs in the winter season, probably largely because of the lack of deciduous foliage.

The foraging pattern of a species is also modified by the presence or absence of unrelated competing species in the flock, there being a tendency for the other

species to fill in any unused parts of the habitat. The niche will be wider for a species if one or more of its closest potential competitors are absent. In the Satsuma pine-deciduous area, Brown-headed Nuthatches are an uncommon species, though common in the Longleaf Pines at Fluker. At Satsuma, Pine Warblers, though not present in large numbers, have a distinct tendency to forage more often in the outer parts of pine branches than in forests frequented by Brown-headed Nuthatches in abundance (Table VI). Conversely, the foraging behavior of Brown-headed Nuthatches often appears dependent upon the presence of Pine Warblers, and perhaps other flock members as well (Table VII).

Correlation between the foraging behavior of the individual and the availability of food is rather close. However, not all the available resources are completely utilized by the resident members of the flock. Flying insects are unavailable to the insect eaters over long periods of time in the northern winter, though abundant and utilized heavily during the summer. In the northern flocks, all the regularly flycatching species are migratory ones. The warblers fit into this category. Though most of the members of northern flocks flycatch at times, comparatively few observations of this habit will be recorded among the winter members of the group even during the late summer and fall. At this time an

TABLE VI

FREQUENCIES (IN PERCENTAGES) ACCORDING TO FORAGING PLACEMENT OF PINE WARBLERS IN MIXED-SPECIES FLOCKS IN LOUISIANA FROM OCTOBER TO MARCH[1,2]

Foraging Position	Pine-deciduous[3]		Pine[4]	
Ground and herb	0.0	(0)	1.4	(7)
Shrub and thicket	0.0	(0)	0.6	(3)
Vine	0.0	(0)	0.0	(0)
Small branches[5]	56.5	(26)	23.7	(118)
Large branches	32.6	(15)	64.0	(318)
Bole	10.9	(5)	10.3	(51)
Totals		46		497

[1]Years 1963-64, 1964-65
[2]The numbers of birds is enclosed in parentheses.
[3]Satsuma study area.
[4]Fluker study area. Includes oak understory.
[5]Includes fruits, cones, and foliage.

TABLE VII

FREQUENCIES (IN PERCENTAGES) ACCORDING TO FORAGING PLACEMENT OF BROWN-HEADED NUTHATCHES IN LONGLEAF PINE FOREST IN LOUISIANA FROM OCTOBER TO MARCH[1,2,3]

Foraging Position	In mixed-species flocks		In pure flocks	
Ground and herb	0.8	(0)	0.3	(2)
Shrub and thicket	0.0	(0)	0.0	(0)
Vine	0.0	(0)	0.0	(0)
Small branches[4]	41.8	(151)	26.6	(166)
Large branches	25.8	(93)	33.7	(210)
Bole	14.4	(52)	29.0	(181)
Cones	17.2	(62)	10.4	(65)
Totals		361		624

[1]Fluker study area.
[2]Years 1963-64, 1964-65.
[3]The number of birds is enclosed in parentheses.
[4]Includes fruits and foliage.

abundance of aerial food exists. It appears more feasible for regularly flycatching species to migrate than to change habits. The habitat may not contain any potential food sources that these species could utilize in the winter. Many trees drop their leaves in the fall, depriving these species of a potential major foraging area. However, evidence of the ability to flycatch may be found even in the Brown Creeper, not usually consedered a flycatching species, which can quite adroitely chase and capture food that it has flushed from the trunks and limbs. Few species that are prominent members of the winter flocks in Louisiana forage regularly at any time of the year by flycatching, though such members are more numerous in these flocks than is the case with northern flocks. In southeastern Louisiana insects are frequently in flight during the cold season, though flying insects do not form a reliable winter food source there. Species regularly flycatching in these flocks and remaining through the winter are the Pine Warbler and Myrtle Warbler, the latter species being a loose associate. The Myrtle Warbler is able to live on a largely vegetable diet, while the Pine Warbler is an efficient forager in the heavy bark of the large pines. Foliated tropical areas probably always contain flying insects and the majority of the northern summer flycatching species winter there. Thus, for flycatching birds

the tropics would have feeding opportunities not present throughout the year in the other two areas.

Most of the other summer members of the northern mixed flocks winter in the tropics also. Perhaps the great influx of these birds places an added premium on flocking in some of these areas because of the density pressure involved when the winter members are there.

A seasonal source of food may be utilized more efficiently by a seasonal form that leaves at a time approximating roughly the time of diminution in such a food supply. Otherwise, a nonmigratory, or nearly nonmigratory, form with a wide food spectrum would be the most likely candidate to utilize this food supply. Nomadic cone-feeding and frugivorous flocks follow their food source as the migrants do.

The late summer-fall faction of the flock, which includes many warblers, is large in number and its members are generally less diversified in their habits and habitats, despite the differences mentioned earlier. Though the food supply appears adequate, a relatively great amount of hostile behavior is to be noted among them, perhaps largely due to the similarity of their niches. These species also may be in competition with the winter members to varying degrees, and may cause most of the antagonistic reactions to be observed between the two groups. The Black-and-White Warbler initiates

a great number of such reactions. Many of the aggressive species are closely related, an additional factor causing a tendency toward hostile behavior. They breed later than the permanent residents, and exhibit a greater amount of post-breeding reproductive behavior such as songs and displays than do the permanent residents.

In some cases, closely related species occur regularly in mixed flocks with a lower level of antagonistic behavior being displayed than in flocks containing many warblers. This state of affairs is illustrated by the European titmouse flocks, where several species regularly occur together. The members show a definite and significant division into distinct niches, except during times of temporary superabundance of food, as when the beech mast ripens. Here the situation appears more advanced than in the warblers previously discussed.

Each flocking species shows a tendency to remain within a characteristic vertical range. This fact has been remarked upon by several investigators and was observed in all flocks that I studied. The vertical dimension in the Maine study generally extended from the understory to the birch top level. In the Louisiana areas this dimension sometimes extended from the understory to the treetops, though not regularly that high.

Only occasionally are flock members widely separated vertically. On 24 January 1965, a small flock consisting

of two Carolina Chickadees, one Golden-crowned Kinglet, one Brown Creeper, and one White-eyed Vireo was studied on the Satsuma plot. All but the creeper were foraging 50 feet or higher in the pine and deciduous trees. The creeper was observed working 10 to 15 feet up the trunks of the same trees in which the other species were foraging. Though this height range is customary for the creeper, this species normally tends strongly to forage at a higher level when other species are also in a higher position.

Each flock member usually ranges through a limited stratum, spending most of its time working horizontally and keeping up with the flock, as well as avoiding conflict with, and encroachment upon, other flock members. Most species that are strong flockers primarily move horizontally. Species that do not move in this manner include Brown Creepers, White-breasted Nuthatches, and some woodpeckers. It will be noted that these species are largely trunk foragers and are utilizing a discontinuous habitat that has more continuity vertically than horizontally. For this reason perhaps, some of them frequently fall behind, as noted by many investigators. As a result, they do not form as integral a part of the flock as the conventionally foraging species. While the White-breasted Nuthatch and Brown Creeper utilized largely vertical habitats, they frequently would move

on with the flock without completing their investigations of the trunk upon which they were foraging. Often these two species would work no more than 10 feet vertically before moving on with the flock, thus perhaps compensating for their basically vertical habitat. The only woodpecker sharing this habit of moving rapidly on with the flock was the Downy, a species that is much more closely attached to the flocks than the larger woodpeckers occurring in the temperate areas studied.

Most species that form insectivorous mixed-species flocks move at least partly above this level join these flocks only temporarily, if at all. They include the heavily vegetarian sparrows, the wrens, and Yellowthroats. While sometimes temporarily involved in flock activity, they would not follow a flock far and would stick closely to the undercover. This type of behavior is reported from many other regions and appears to be a general phenomenon.

The Carolina Wren is conspicuous in the areas studied in Louisiana. It possesses a number of loud calls, including a rasping scold note somewhat suggestive of the calls of the Tufted Titmouse. Seldom have I seen other species strongly attracted to any of the wren displays. Titmouse calls of comparable intensity would have evoked a strong response from flock members. Carolina Wrens are strongly attracted to other species

such as the Tufted Titmouse and Carolina Chickadee and will often begin to sing when they become very excited. This behavior would serve as a disruptive element in a flock. The bird's lack of call notes that attract, together with its tendency to sing frequently, to remain on a confined territory, and to stay in the underbrush combine to prevent it from becoming an important flock participant. When near mixed tanager flocks in Costa Rica, Plain Wrens and Riverside Wrens behaved in a similar manner, frequently breaking into song at moments of maximum stimulation.

Winter Wrens and Yellowthroats are frequent members of the late summer-fall flocks in Maine, both remaining in the underbrush, and do not usually follow the groups for substantial distances. At this time of year these two species seldom sing.

Sparrows are occasionally attached to mixed-species flocks. White-throated Sparrows are sometimes associates, but they usually remain low in the foliage also. More often they form their own flocks. They were observed about both the late summer-fall flocks in Maine and the flocks in Louisiana, not differing noticeably in their behavior and ecology. The previously mentioned Chipping Sparrows, Slate-colored Juncos, and Eastern Bluebirds have a tendency to follow mixed flocks in

the Louisiana Longleaf Pine forest, particularly in the more open areas.

I made winter bird population studies of a deciduous forest, a mixed pine-deciduous forest, and a Longleaf Pine forest in Louisiana following the procedure utilized by Audubon Field Notes. The totals were not rounded off. These studies indicated that the over-all population density of birds is lowest in the pure pine forest, intermediate in the mixed forests, and highest in the deciduous ones (Table VIII). On the average, flocks were largest in the Longleaf Pine forests (Table IX), indicating a definitely greater tendency to flock in areas supporting a low density of birds. Here the distance between flocks was greater than in the other two study areas. Writers such as Bates (1864:403), Chapin (1932), Rand (1936), and Stanford (1947) have described the rapid movement of flocks through the nearly silent tropical forest, in which they had previously seen scarcely a bird and in which they saw few afterward. A somewhat similar situation existed in the Longleaf Pines, as the flocks were widely spaced and the majority of the pineland birds were concentrated into these flocks. The Longleaf Pine area contained the largest percentage of strongly flocking birds of any of the three areas surveyed (Table X). Finally, several of the flocking species found in all three study areas

TABLE VIII

DENSITY (PER 100 ACRES) OF BIRDS IN LOUISIANA STUDY AREAS DURING WINTER OF 1964-65[1]

Species	Deciduous[2]	Pine-deciduous[3]	Pine[4]
Red-tailed Hawk	-	0.5	-
Sparrow Hawk	-	-	1.7
Bobwhite	-	-	0.3
Flicker	3.3	2.9	0.3
Pileated Woodpecker	-	2.4	-
Red-bellied Woodpecker	12.0	10.0	3.0
Red-headed Woodpecker	-	11.0	-
Yellow-bellied Sapsucker	6.0	5.7	0.3
Hairy Woodpecker	2.7	0.5	0.3
Downy Woodpecker	9.3	5.2	0.3
Red-cockaded Woodpecker	-	-	1.3
Eastern Phoebe	5.3	3.8	-
Blue Jay	2.7	4.3	1.3
Common Crow	-	0.5	-
Carolina Chickadee	18.7	19.0	4.7
Tufted Titmouse	14.7	14.0	7.0
White-breasted Nuthatch	-	-	0.7
Brown-headed Nuthatch	-	-	17.2
Brown Creeper	5.3	4.7	2.3
House Wren	-	1.0	-
Winter Wren	-	1.4	-
Carolina Wren	26.7	26.7	1.7
Mockingbird	6.0	2.9	-
Catbird	-	1.0	-
Brown Thrasher	0.3	4.3	-
Robin	37.3	6.7	0.7
Hermit Thrush	2.0	1.0	0.3
Eastern Bluebird	-	-	0.7
Golden-crowned Kinglet	8.0	11.9	1.3
Ruby-crowned Kinglet	14.7	12.4	3.7
White-eyed Vireo	-	1.0	-
Orange-crowned Warbler	-	1.4	-
Myrtle Warbler	49.3	1.9	1.0
Pine Warbler	3.3	9.1	9.3
Yellowthroat	1.3	-	-
House Sparrow	1.3	-	-
Redwinged Blackbird	20.0	-	-
Common Grackle	4.0	-	-

TABLE VIII (continued)

Species	Deciduous	Pine-deciduous	Pine
Cardinal	36.7	16.2	0.3
American Goldfinch	-	-	0.3
Rufous-sided Towhee	-	6.2	0.3
Bachman's Sparrow	-	-	4.3
Slate-colored Junco	-	-	1.0
White-throated Sparrow	46.7	39.6	0.3
Swamp Sparrow	1.3	-	-
Totals	338.9	229.2	65.9

[1]Based on average of six censuses between 12 December and 31 January.
[2]Baton Rouge study area 25 acres.
[3]Satsuma study area. 35 acres.
[4]Fluker study area. 50 acres.

adhered to flocks most strongly in this area (Table XI). The mixed pine-deciduous forest was intermediate to the Longleaf Pine forest and deciduous forest in most of these factors. However, flocks in the deciduous tract were somewhat larger than in the mixed pine-deciduous study area. The condition on the deciduous tract is largely attributable to the presence of many migrants in the fall and large numbers of the rather loosely flocking Myrtle Warbler in the winter.

The tendency for larger flocks to be formed, for the flocks to be more widely spaced, for a larger percentage of strongly flocking birds to be present, and for flocking species to stick more tenaciously to flocks in the area supporting the lowest density of birds suggests that an improved energy condition is an important function of flocking. Pure coniferous forests usually support noticeably low concentrations of winter bird life, as can be ascertained by recourse to the winter bird population studies found in Audubon Field Notes.

Differences in the rate of foraging vary with the species and season. The activity was rather leisurely in late summer and fall, but increased in the winter, and in the case of the small forms, steady foraging occurred almost all the day during cold spells in mid-winter. In Black-capped Chickadees increased foraging in winter has been remarked upon by Odum (1942).

Lawrence (1958), and Brewer (1961). Brewer also noticed this change in foraging rate in the Carolina Chickadee.

Gibb (1960) found that in some habitats the birds eradicate high proportions of the invertebrate food stock over the period of the winter. In English pine plantations he determined that up to 77 per cent of the major species in the birds' diets were removed by the end of the winter. MacLellan (1961) found that Hairy and Downy Woodpeckers captured over 52 per cent of all the Codling Moths (Carpocapsa pomonella) in some Nova Scotia orchards. Lack (1954:141-144) had earlier indicated that the percentage of the total prey taken by predators was considerably lower, though few of his figures related to the critical winter season. However, he cited evidence that had led him to believe that birds were limited in numbers by their food supply.

The actual existence of an adequate food supply may not always be the immediately critical problem. Some potential food items may be unavailable because of their position beyond the reach of the birds. This problem is extremely critical where the weather is constantly so cold that insects remain dormant for extended periods. In addition, food items may not be readily enough obtainable for a sufficient number to be procured in the time available each day. Gibb's Goldcrest populations in the pine plantations must have barely obtained the

necessary amount of food in the mid-winter, since they foraged almost constantly during that part of the year. He estimated that if they foraged 90 per cent of the time, they would have to obtain a little more than two milligrams dry weight of food every 24 seconds, the average amount of time that they remained in a single tree. He also found that the smaller the species, the greater the percentage of time that it foraged. Thus, while Goldcrests foraged nearly continually through the daylight hours under mid-winter conditions, other larger species spent less of their time engaged in this activity. Illustrative foraging times of the other species were: Long-tailed Tit, 95 per cent; Coal Tit, 90 per cent; Blue Tit, 85 per cent; and Great Tit, 75 per cent.

Such an energy problem may partly account for the extremely large foraging areas of the Lapp Tit and Willow Tit in Lapland during the winter described by Snow (1952). Here the day is short, the weather cold, and a heavily foraged area may be unable to yield the necessary resources in the restricted time available. Probably neither of these species could tolerate a great increase in competition under such conditions.

While the flock members in Louisiana are seldom exposed to conditions comparable to those continually facing northern flocks, they probably are not as well

TABLE IX

SIZE OF MIXED-SPECIES FLOCKS IN LOUISIANA DURING THE FALL AND WINTER SEASONS OF 1963-64 AND 1964-65[1]

Month	Deciduous[2]	Pine deciduous[3]	Pine[4]
October	15.0 (2)	8.2 (13)	23.4 (10)
November	18.8 (5)	16.2 (17)	26.4 (20)
December	14.2 (5)	10.8 (4)	22.5 (6)
January	10.1 (8)	12.1 (18)	22.4 (21)
Totals	13.8 (20)	12.3 (52)	24.1 (57)

[1]The number of flocks is enclosed in parentheses.
[2]Baton Rouge study area.
[3]Satsuma study area.
[4]Fluker study area.

TABLE X

FLOCKING TENDENCIES OF BIRDS IN TABLE VIII IN PERCENTAGES[1]

Category	Deciduous	Pine-deciduous	Pine
Passive nuclear[2]	9.9 (33.4)	14.4 (33.0)	17.8 (11.7)
Other strong flockers[3]	12.0 (40.6)	18.8 (43.2)	53.6 (34.8)
Moderate flockers[4]	20.7 (70.0)	9.0 (20.5)	9.1 (5.9)
Nonflocking[5]	57.4(194.9)	57.8(132.5)	19.5 (13.5)

[1]Population density of birds per 100 acres in parentheses.

[2]Carolina Chickadee and Tufted Titmouse.

[3]Downy Woodpecker, White-breasted Nuthatch, Brown-headed Nuthatch, Brown Creeper, Golden-crowned Kinglet, Ruby-crowned Kinglet, and Pine Warbler.

[4]Red-bellied Woodpecker, Yellow-bellied Sapsucker, Hairy Woodpecker, Red-cockaded Woodpecker, White-eyed Vireo, Orange-crowned Warbler, and Myrtle Warbler.

[5]All other species in Table VIII.

TABLE XI

PERCENTAGES OF TIMES SPECIES WERE OBSERVED IN MIXED-SPECIES FLOCKS IN LOUISIANA DURING THE FALL AND WINTER SEASONS OF 1963-64 AND 1964-65[1,2,3,4]

Species	Deciduous[5]	Pine-deciduous[6]	Pine[7]
Red-bellied Woodpecker	18.2(11)	41.7(24)	69.2(26)
Yellow-bellied Sapsucker	0.0 (6)	30.4(23)	0.0 (4)
Hairy Woodpecker	0.0 (2)	100.0 (1)	71.4 (7)
Downy Woodpecker	63.6(11)	78.9(19)	83.2(12)
Red-cockaded Woodpecker	-	-	61.1(18)
White-breasted Nuthatch	-	-	75.0 (8)
Brown-headed Nuthatch	-	100.0 (1)	39.7(73)
Brown Creeper	100.0 (7)	100.0(12)	92.9(14)
Golden-crowned Kinglet	80.0 (5)	85.7(21)	100.0(13)
Ruby-crowned Kinglet	30.0(30)	44.7(38)	65.9(29)
White-eyed Vireo	-	100.0 (2)	-
Orange-crowned Warbler	-	66.7 (3)	-

[1]The number of observations is enclosed in parentheses.

[2]Because of the great number of times that Myrtle Warblers were seen spaced through the habitat, it was difficult to obtain a meaningful tally.

[3]Because of the large number of Pine Warblers exhibiting reproductive behavior from 1 January on, no meaningful tally could be obtained.

[4]These data were obtained on days in which the total number of sightings of the species in question in and away from a flock was accurately recorded. Some days other phases of the study made counting of all individuals of a species, in a flock and away from it, feasible. As a result the total number of observations

TABLE XI (continued)

tallied in this table and in Table XII does not usually coincide. In this table and in Table XII the sightings in the flocks are the result of careful checking, which was accompanied by the taking of extensive notes on the behavior and ecology of the species concerned.

[5]Baton Rouge study area.

[6]Satsuma study area.

[7]Fluker study area.

TABLE XII

PERCENTAGES OF MIXED-SPECIES FLOCKS IN LOUISIANA CONTAINING CERTAIN SPECIES DURING THE FALL AND WINTER SEASONS OF 1963-64 AND 1964-65[1,2]

Species	Deciduous[3]	Pine deciduous[4]	Pine[5]
Red-bellied Woodpecker	25.0 (8)	38.5(26)	56.3(32)
Yellow-bellied Sapsucker	0.0 (8)	28.0(25)	0.0 (9)
Hairy Woodpecker	0.0 (3)	33.3 (3)	27.8(18)
Downy Woodpecker	87.5 (8)	75.0(20)	50.0(12)
Red-cockaded Woodpecker	-	-	40.7(27)
White-breasted Nuthatch	-	-	50.0(12)
Brown-headed Nuthatch	-	25.0 (4)	100.0(29)
Brown Creeper	58.3(12)	63.2(19)	59.1(22)
Golden-crowned Kinglet	50.0 (8)	64.3(28)	65.0(20)
Ruby-crowned Kinglet	50.0(12)	60.7(28)	86.4(22)
White-eyed Vireo	-	25.0 (8)	-
Orange-crowned Warbler	-	20.0(10)	-
Myrtle Warbler	70.0(10)	29.4(17)	34.5(29)
Pine Warbler	40.0 (5)	47.1(17)	93.8(16)

[1]The number of flocks is enclosed in parentheses.
[2]These data are extracted from my field notes and represent only instances in which an accurate count of all species present in a flock was obtained.
[3]Baton Rouge study area.
[4]Satsuma study area.
[5]Fluker study area.

equipped as northern individuals to withstand the rigors of a cold environment (see Scholander, 1955). As a result, unusual cold or storms may place more severe demands upon them than comparable weather does upon the northern populations.

Since animals cannot survive indefinitely in an area in which they cannot maintain a positive energy balance, and since flocking appears to represent a more efficient means of foraging, it probably permits a greater geographical and ecological range than would be possible otherwise in some species. I have already noted that there is a stronger tendency for birds to flock in the Longleaf Pine forest than in other Louisiana areas studied. One might thus expect a species to show a greater tendency to flock along the geographical edges of its range that are defined by a relatively unsatisfactory energy balance brought about largely by a scarcity of food. As stated earlier, Carolina Chickadees and Tufted Titmice probably show less tendency to defend a territory along the northern edges of their ranges. The Great Tit clearly demonstrates such a pattern (see Hinde, 1952).

When pine seeds are available, they become an important item in the diet of some flock species. Some observations of birds feeding on cones may involve insect probing. However, the majority of such observations

made in the Longleaf Pine forests during the 1964-65 season at the time of heavy seed production were of birds that successfully procured seeds. Norris found that Brown-headed Nuthatches in Georgia fed heavily upon Longleaf Pine seeds during winter months. Burleigh (in. litt.) states that pine seeds are the preferred food of Brown-headed Nuthatches when available. I found that Brown-headed Nuthatches fed more frequently upon pine seeds than any other mixed flock species in the Longleaf Pine forest (see Table XIII).

A Brown-headed Nuthatch specimen taken on 11 November 1964 showed the intermediate step in food change from animal matter to pine seeds. It contained approximately 50 per cent sawfly larvae (Diprionidae) and 50 per cent Longleaf Pine seeds by bulk. At this time the foraging behavior of Brown-headed Nuthatches was showing signs of change (see Table XIV).

Utilization of pine seeds by Brown-headed Nuthatches requires a modification of their spatial distribution. Removing seeds from cones does not necessitate any radical changes, because the outer part of the high pine foliage where most of the cones are situated is heavily utilized by this species at all times. However, to crack and open pine seeds successfully, the nuthatches have to insert them into crevices of the bark and hammer upon them with their bills. The only crevices that

TABLE XIII

VISITS TO LONGLEAF PINE CONES BY SPECIES IN MIXED-SPECIES FLOCKS IN LOUISIANA DURING THE FALL AND WINTER OF 1963-64 AND 1964-65[1,2]

Species	1963-64		1964-65	
	Number of foraging observations on cones	Percentage of total foraging observations	Number of foraging observations on cones	Percentage of total foraging observations
Brown-headed Nuthatch	2	3.7 (54)	60	19.5 (307)
All other species	2	0.5 (415)	99	7.3 (1354)

[1]The number of birds is enclosed in parentheses.
[2]Fluker study area.

TABLE XIV

FREQUENCIES (IN PERCENTAGES) ACCORDING TO FORAGING PLACEMENT OF BROWN-HEADED NUTHATCHES IN LONGLEAF PINES IN LOUISIANA DURING FALL AND WINTER OF 1964-65[1,2]

In mixed flocks

Foraging Position	October	November	December	January
Small branches[3]	77.3 (34)	52.5 (73)	21.0 (12)	28.3 (17)
Large branches	9.1 (4)	22.3 (31)	28.1 (16)	28.3 (17)
Bole	2.3 (1)	12.7 (17)	15.8 (9)	15.0 (9)
Cones	11.3 (5)	13.0 (18)	35.1 (20)	28.3 (17)

In pure flocks

Foraging Position	October	November	December	January
Small branches[3]	-	26.1(109)	29.5 (38)	27.9 (19)
Large branches	-	35.9(150)	30.2 (39)	30.9 (21)
Bole	-	30.1(126)	17.8 (23)	36.8 (25)
Cones	-	7.9 (38)	22.5 (29)	4.4 (3)

[1]The number of birds is enclosed in parentheses.
[2]Fluker study area.
[3]Includes foliage.

appear large or deep enough for this purpose are on the rougher, scalier, more ridged bark found on the trunk and larger limbs. Occasionally, individuals were seen attempting to crack seeds farther out on the limbs, but their efforts seemed unsuccessful. Like Norris (1958), I did not observe any nuthatches using their feet to aid in holding seeds as titmice do. With only one exception, the contents of the 21 stomachs I examined indicated that Brown-headed Nuthatches shelled the seeds before swallowing them.

Previous to the heavy utilization of pine seeds in mid-November, when Brown-headed Nuthatches and Pine Warblers occurred in mixed flocks, Brown-headed Nuthatches showed a strong tendency to do the major part of their foraging on the small pine limbs and foliage (Tables VII and XIV). When in pure flocks they showed a marked tendency to forage heavily on the trunks and large limbs of the pines (Tables VII and XIV). Pine Warblers utilized most heavily the proximal parts of the limbs where a substantial amount of scaly bark was to be found (Tables VI and XV). They would even cling to pine trunks and hitch about on them, if only clumsily. This division of habitat was most pronounced when approximately even numbers of both species were present in a flock.

The behavior of Brown-headed Nuthatches within the flocks became quite similar to their behavior away from

the flocks in contrast to the differences exhibited in the first part of the season and in the 1963-64 winter. Table XIV shows the similarities in foraging position then apparent. Increased contact with such forms as the Pine Warbler was accompanied by an increase of interspecific hostile behavior. The Pine Warbler is usually a more aggressive species than the nuthatch. Its attacks, often launched from a considerable distance and with wings spread, represent a more impressive and formidable stimulus in a confrontation than those of the Brown-headed Nuthatch, which usually are simple supplanting attacks. In consequence, the Pine Warbler may more often than not prevail. However, in meetings involving no airborne attack, Brown-headed Nuthatches appear to be the equal or more than the equal of Pine Warblers, as was illustrated in the Loblolly Pines at Satsuma on 26 November 1964. A probable resident Pine Warbler approached two nuthatches, displaying slightly. The Pine Warbler was supplanted almost immediately by one of the nuthatches when the former had reached a distance of two or three feet.

This aggressiveness probably enables the Pine Warbler to maintain its position on the inner parts of the tree, in the region of the larger bark scales. The complementary foraging positions of this species and the Brown-headed Nuthatch appear almost paradoxical, as many

TABLE XV

FREQUENCIES (IN PERCENTAGES) ACCORDING TO FORAGING PLACEMENT OF PINE WARBLERS IN MIXED-SPECIES FLOCKS IN LONGLEAF PINES IN LOUISIANA DURING FALL AND WINTER OF 1964-65[1,2]

Foraging Position	October	November	December	January
Small branches[3]	11.1 (4)	14.0 (8)	22.0 (17)	25.2 (59)
Large branches	86.1 (31)	71.9 (41)	65.0 (50)	61.1(143)
Bole	2.8 (1)	12.3 (7)	7.8 (6)	12.4 (29)
Cones	-	1.8 (1)	5.2 (4)	1.3 (3)

[1]The number of birds is enclosed in parentheses.
[2]Fluker study area.
[3]Includes foliage.

species of nuthatches forage principally on the trunk and larger limbs rather than in the foliage and small limbs. The Pine Warbler is very adept at hopping rapidly along the large horizontal limbs near the trunks and can scale bark off these limbs nearly as effectively as a Brown-headed Nuthatch. It can hang upside down on a horizontal limb much as a chickadee does, though it is not nearly as adept at this action. As mentioned previously, it also is able to forage on trunks.

A somewhat lesser tendency for Pine Warblers to forage on the large limbs was noted as the period of the large pine seed crop progressed (see Table XV). The change might have been partly a result of the increased use of the large limbs and trunk for seed cracking and other foraging activities by the Brown-headed Nuthatches in mixed flocks. The warblers might also have been utilizing the most accessible food sources at the time. Insufficient observations were made on Pine Warblers away from mixed flocks to throw much light on this problem, but the pattern at Satsuma, where Brown-headed Nuthatches are rare would suggest that this slight change in foraging behavior might be the result of the change in the behavior of the nuthatches.

It was perhaps significant that the use of tools, a behavioral characteristic not previously recorded for the Brown-headed Nuthatch in the literature, was

observed only during periods when these birds were not feeding extensively on pine seeds. The use of tools in Brown-headed Nuthatches consisted essentially of selecting a piece of bark from the extremely scaly trunk on inner limbs and using it as a lever to pry off another scale of bark. This being done, the lever was dropped and the area freshly bared was investigated for possible food particles. The tools observed were four to eight times the width of the nuthatch bill and projected one to two times the length of the bill beyond its tip.

While not a particularly prevalent activity, this behavior was not rare, and could be seen many days in the 1963-64 and early 1964-65 seasons if one watched patiently. I did not note any tool use during my rather brief look at this species in the Satsuma pine stands. Loblolly and Spruce Pines do not possess quite as scaly bark as the Longleaf Pine. Perhaps the use of tools is a local behavioral characteristic. I was not the first to note this behavior, as Mr. S. L. Warter informed me of his earlier observations of the phenomenon in this general area of Longleaf Pines.

The use of probes is of importance, at least in the population studied, for foraging in areas with heavy bark. Such bark presents a myriad of possible hiding places for insects. However, foraging observations

indicate that this species spends a large proportion of its time on smaller branches and out into the foliage, where the use of such instruments would be impractical because of the scarcity or lack of scaly bark. As a result tool use is only occasionally noted.

The observer must be careful not to confuse tool using with the cracking of the pine seeds, which in the Longleaf Pine are large and prominently winged, somewhat comparable in shape and size to some maple (Acer) seeds. I was able to retrieve the tool on two occasions to verify that the element dropped was a piece of bark rather than a seed that had been wedged into the bark for opening. Some tools are so large that the possibility of their being seeds is precluded.

In the heavy seed year, Brown-headed Nuthatches appeared to become less strongly affiliated with the Carolina Chickadee-Tufted Titmouse groups as the season progressed through December and early January. Because of its behavioral characteristics, this nuthatch was frequently found away from mixed flocks and when with them showed a tendency to break away. There is some evidence to indicate that in the presence of the big cone crop this affiliation was even more transitory than usual. In Table XVI the observations on 6 November are typical of the customary condition, while the

observations of 7 and 16 December illustrate the change when the pine seeds become available for food. Normally, the nuthatches are strongly attracted to the loud scold notes of the chickadees and titmice in territorial disputes; during the period of cone abundance this tendency appeared less pronounced. Sometimes the nuthatches paid almost no attention to these calls, though complete indifference almost never occurred.

The strong tendency for Brown-headed Nuthatches to feed heavily upon a single cone or few cones within a restricted area limited their movements considerably for as long as several minutes at a time. On such occasions they were left behind and became separated from the flock more readily. At other seasons, the foraging speed of the nuthatches had been such that they frequently showed a tendency to move ahead of and eventually away from a mixed flock, rather than to be left behind. Dropping behind occurred when remaining in the flock would have involved maximum contact with Pine Warblers. Lowered participation in mixed flocks would lessen this disharmonious factor. Also, if the food supply is superabundant, advantages of moving with a flock for the purposes of feeding may be limited Since the nuthatches use the pine seeds more extensively than any other species in the pineland flocks, advantages for them in mixed flocking might then be minimal.

TABLE XVI

OBSERVATIONS OF BROWN-HEADED NUTHATCHES IN AND AWAY FROM MIXED-SPECIES FLOCKS IN LONGLEAF PINES IN LOUISIANA DURING THE 1964-65 SEASON[1]

Date	Flocks with nuthatches	Number of times nuthatches seen away from flocks
6 November	3	4
29	4	2
7 December	3	9
16	3	10
4 January	3	7
11	3	2
17	3	3
23	2	1
30	5	6

[1]Fluker study area.

The foraging of Brown-headed Nuthatches on cones differs from normal flock foraging in that a continual movement is not kept up. Continual movement results in the gleaning of a very small percentage of the available food from one given area at a time. The nuthatch foraging on an abundant crop closely resembles the type of modification observed in flocks of seed-eating fringillids and some frugivorous species. Though abundant, the cones did not all ripen simultaneously, and pure flocks may have aided in food search.

Although there was no indication of a sizeable influx of Brown-headed Nuthatches into the study area, groups of these birds away from the mixed flocks at the height of pine seed utilization often were smaller, frequently consisting of one to three birds, therefore the birds were more spread out over the habitat than previously. These small groups may have been birds that had broken off from the bigger pure flocks and mixed flocks because of a tendency to lag behind and feed on single cones or cone clusters. Though not as closely attached to the mixed flocks at this season, the nuthatches were found in all mixed chickadee-titmouse flocks that were tallied in the Longleaf Pine study area during the period. As the supply of seeds began to fail in some parts of the forest in January, the scattering became less evident (see Table XVI).

Several other species fed upon Longleaf Pine seeds, though Brown-headed Nuthatches utilized them most heavily. Other species seen procuring seeds from cones included the Red-bellied Woodpecker, Carolina Chickadee, Tufted Titmouse, White-breasted Nuthatch, and Pine Warbler.

How much the Pine Warblers depended upon pine seeds is questionable. Though five specimens taken on 11 January 1965 contained an average of 45 per cent pine seeds, this figure was not approached at any other time. On this date extensive foraging on the ground, a rare occurrence for this species, was observed. More than one-half of the pine seeds recovered were tender green sprouts, which apparently had been picked up off the ground, where they had begun to germinate.

Pine Warblers were inefficient in opening hard pine seeds in the trees. One was observed working on a seed at least five minutes in three different locations, all on horizontal limbs fairly near the trunk. The method utilized was similar to that of the Brown-headed Nuthatches, wedging the seed in a crevice of the bark and hammering upon it. However, the Pine Warblers were not nearly as adept at this practice as the Brown-headed Nuthatches. On at least two occasions, Pine Warblers were observed to light on a pine cone, pull out and drop two or more seeds, then continue to probe actively. Perhaps they were searching for insects or other animal

food there. One of the seeds that was dropped proved upon inspection to be an average-sized meaty one.

Carolina Chickadees and Tufted Titmice were observed foraging more heavily upon the pine seeds than any other species except the Brown-headed Nuthatch. Even though food supply was superabundant, a number of observations of Brown-headed Nuthatch hostility toward chickadees were made. At the time of the year when cones are not being utilized, the chickadees rarely reach any great height in the pine cover and to a large extent confine their activities to the scattered deciduous growth. There they spend a great deal of their time gleaning the foliage, frequently capitalizing on their unsurpassed ability to hang upside down, particularly from branch tips.

Tufted Titmice did not begin to utilize the pine seed crop as early as the Carolina Chickadees. The chickadees and Brown-headed Nuthatches had been feeding regularly upon the pine seeds for two weeks or more before titmice were definitely seen to do so. The first observation of a titmouse feeding on pine seeds was made when an individual captured a falling seed in mid-air, much as it would catch an insect. Though Tufted Titmice have been recorded feeding regularly on the ground in some regions, such behavior was not observed in the Longleaf Pine area until this same day (29 November 1964),

when at least two titmice were seen on the ground under pine trees picking up pine seeds. They would take the seeds to low limbs nearby and crack them. Eight days later an observation was made of a titmouse foraging at a pine cone. On later dates, this species was not infrequently seen working the cones.

The tendency to utilize a single cone or cone cluster for a long interval did not appear so marked in the chickadees and titmice as in the Brown-headed Nuthatch; their forward movement tended to be smoother and more constant. Since the chickadees and titmice are the passive nuclear species, a flock would have a greater tendency to remain about them than about the Brown-headed Nuthatches, even if the chickadees and titmice were not moving from place to place regularly.

The White-breasted Nuthatch was seen feeding heavily upon pine seeds on one occasion, the seeds being procured from cones on the lower branches. The tendency for Brown-headed Nuthatches to be found more frequently on the pine trunks when in the process of cracking seeds led to increased contact with the White-breasted Nuthatches, with an increased amount of hostile behavior. The Brown-headed Nuthatch most frequently instigated this behavior, but the larger White-breasted Nuthatch always appeared to prevail. The White-breasted Nuthatch is not a common inhabitant of the Longleaf Pine forests, and it usually

devotes the majority of its foraging efforts to the lower parts of the pine trunks.

While in seasons of abundance the pine seeds form an important part of the diet of many species, they are not utilized by others, such as Golden-crowned and Ruby-crowned Kinglets. The seeds almost never form more than part of the diet of any of the flock species, with the exception of the Brown-headed Nuthatches at certain times.

Though many of these birds feed heavily upon Long-leaf Pine seeds, this species of pine is an extremely unpredictable producer, bearing only one excellent crop every five to seven years, and having complete failures about one year in five (Wahlenberg, 1946:72). Even in the 1964-65 season the crop was not sufficient to feed many of the individuals through January. By mid-January, cone foraging had begun to decline, and several observations were made of Carolina Chickadees and Brown-headed Nuthatches searching unsuccessfully through two or three cones in rapid succession. A tendency toward the type of foraging employed before the seed crop became available could now be detected. By 7 February 1965, stomach contents disclosed a much lower percentage of pine seeds in the stomachs of all species (see Table XVII). At this time, only scattered cones remained that contained seeds. Two of the Brown-headed Nuthatches taken on 7 February

were from an area that still contained an ample supply of seeds. The stomach contents of these birds were strikingly different from the others taken that day, and were almost completely filled with pine seeds. Other individuals of this species taken one-fourth mile away contained a much lower percentage of pine seeds and a considerable amount of insect matter.

Burleigh (in litt.) found that Brown-headed Nuthatches would often leave a pine area without cones and congregate in other species of pines that had produced a crop. However, Brown-headed Nuthatches are rather sedentary, as stated by Norris (1958) and confirmed by my own experience. Perhaps in such an extensive area of homogeneous Longleaf Pine as I studied, they do not enjoy ready access to other species of pines. Under such circumstances, this species (and probably the other mixed flock members feeding on these seeds) would not be limited by the supply of the seeds, since the latter are so unpredictable, but rather by the source fed upon in the absence of this undependable food supply. In spite of the abundance of food existing through much of the winter, the population density in this study area remained low. As the season progressed, the numbers of American Goldfinches feeding on pine seeds increased markedly. The possibility of having much of this food supply usurped by nomadic species is another reason

why pine seeds represent a very unreliable source of food.

Beating in mixed woodland flocks may be defined as the act of flushing prey as the members of these flocks move through the foliage. Probably no more than a limited advantage is gained by the beating action of mixed species flocks, though some individuals undoubtedly benefit from it. It is of greatest aid to predominantly flycatching forms and of less use to others. As flock members become more widely spaced, beating will become less effective.

The majority of writers who have indicated that beating is a major benefit obtained from flocking have observed this phenomenon in tropical regions. They have studied flocks in such areas as Africa (Marshall, 1900; Neave, 1910), Madagascar (Rand, 1936), and the Phillipines (McGregor, 1920). When the temperature is so low that insects will not fly, beating is useless. That is why a beating function has its greatest constant potential in tropical areas.

The ability of many species to capture prey that they have flushed or dislodged is greater than the literature indicates. I have frequently observed warblers in late summer-fall flocks in Maine chase dropped or flushed prey from the treetops nearly to the ground and successfully capture it. If an individual often captures

the insects that it personally flushes, the advantage of beating for the flock is decreased. On occasions, even such trunk-foraging species as Red-bellied Woodpeckers and Brown Creepers successfully perform similar feats. In flocks that I observed, a significant percentage of the insects that were put to flight by beating were captured by the individuals that actually flushed them.

ANALYSIS OF STOMACHS

During the 1964-65 season several specimens were procured in areas similar to the study plots, and the food contents of their stomachs were examined. The contents of the stomachs served as a check on the foraging observations; and, though the number of specimens taken was not sufficient for extensive analysis, part of the results are presented in Table XVII. Most of the specimens were obtained in the Longleaf Pine forest at Fluker.

Obviously it was impossible to collect on or adjacent to the study areas, and difficulty was encountered in collecting enough specimens in an adjacent area. In addition, I could not obtain sufficient specimens and compile adequate behavioral records at the same time. Specimens could not be collected without approaching in such a way that the normal behavioral patterns of an individual would be disrupted. One shot was usually sufficient to alter temporarily the behavior of all the individuals in the flock. Thus one can only assume that the foraging patterns of the collected specimens closely

approximated those that were observed satisfactorily and that are reported upon elsewhere in this paper.

A fairly close correlation between the stomach contents and foraging behavior was obtained. The major discrepancy lay in the amount of time apparently spent foraging over trunks, limbs, and foliage by such species as the Brown-headed Nuthatch during the period of maximum Longleaf Pine seed abundance and the scarcity of animal matter contained. The conspicuous presence of green pine seed shoots in the stomachs of Brown-headed Nuthatches and Pine Warblers correlated closely with the greatly increased ground foraging noted on 17 January 1965.

Stomach contents indicate that the food habits of these flocking birds varied conspicuously from area to area. This variability became extremely noticeable when the Longleaf Pine seed supply began to fail noticeably in January 1965. By 7 February, seeds remained only in widely scattered patches. Stomachs of Brown-headed Nuthatches contained from 30 per cent to 100 per cent pine seeds at this time, depending upon the local stock still available.

Hartley (1953) states the shortcomings of stomach analysis as a means of studying ecological relationships:

> The discovery of the same food organisms in all the species examined does not prove interspecific competition, unless it be also proven that all the predator species have investigated all the sources

TABLE XVII

PERCENTAGE OF VEGETABLE MATTER (BY VOLUME) IN STOMACHS OF SPECIES FOUND IN LONGLEAF PINE FOREST IN LOUISIANA DURING THE FALL AND WINTER OF 1964-65[1,2]

Species	23 Oct.	21 Nov.	16 Dec.	11 Jan.	7 Feb.
Carolina Chickadee	-	50(1)	85(2)	-	40(4)
Tufted Titmouse	-	40(1)	85(3)	85(3)	40(2)
Brown-headed Nuthatch	50(1)	99(5)	90(3)	75(6)	65(6)
Pine Warbler	0(1)	25(4)	-	45(5)	5(5)

[1]Fluker region.

[2]The number of specimens examined is enclosed in parentheses.

> of supply with equal diligence and that the stock of food is inadequate for their needs. The finding of different foods in different species is not irrefutable proof of the absence of competition, unless it be shown that all selection of foods is by choice and choice alone from diverse super-abundant food stocks, all equally accessible to all the species studied.

Stomach analyses supported the foraging observations indicating that the Brown-headed Nuthatches were the first to make extensive use of the seed crop. Data obtained by this means were insufficient to determine whether the Carolina Chickadees discovered this source of food sufficiently before the Tufted Titmice, but field observations indicated that such was the case.

The stomach data also indicated that the Brown-headed Nuthatches generally fed more heavily upon pine seeds than did any other species. Several stomachs of this species analyzed contained only pine seeds. In only one other case did an individual of another species have a gut completely full of pine seeds, this individual being a Tufted Titmouse. Very little vegetable matter was found in addition to the pine seeds in any birds taken in the Longleaf Pines.

Animal food was more varied. Several sawfly larvae (Diprionidae) were found in the stomachs of a Pine Warbler taken on 23 October and a Brown-headed Nuthatch taken on 11 November. These larvae were again numerous in the stomachs of birds taken on 7 February 1965 and were occasionally found in other samples taken between

these dates, probably as a result of extended periods of warm weather. Brown-headed Nuthatches and Pine Warblers fed most heavily upon this resource. Unidentified egg cases were a somewhat less prominent food item, being found most frequently in the stomachs of Tufted Titmice. Small Coleoptera formed the most frequent item of animal food. Most of these appeared to be members of the Scolytidae, a family that according to Wahlenberg (1946:168) includes some of the most destructive pests of the Longleaf Pine. Outside of the season of maximum seed abundance, these small beetles were a favored food of the Brown-headed Nuthatch and also were found in the stomachs of Carolina Chickadees, Tufted Titmice, and Pine Warblers. Homopterans (probably small Coccidae) were another major food, especially in January and February when the pine seed consumption began to decrease. They were fed upon by all the species that were analyzed but appeared slightly more prominent in the diet of the chickadee, titmouse, and Pine Warbler than in the diet of the Brown-headed Nuthatch. Other recognizable food elements included unidentifiable spider parts and dipteran wings. The number of insect pests affecting the Longleaf Pines is quite low because of the resinous character of its wood (Wahlenberg, 1946:165); so one would not expect a great variety of species to be found in the diets of the birds. Though differences were

noted in the frequency of food items appearing in the stomachs of the different species, the small variety of prey species regularly utilized indicates that much of the actual niche separation in these insectivorous birds is the result of foraging in somewhat different parts of the habitat, rather than of the birds' selecting different food items.

A somewhat lesser number of specimens were taken in the vicinity of the Satsuma study area. Their stomachs indicated an even greater variety in food habits within a species than did those of the Fluker birds. The greater variety of available food items and the discontinuous nature of this pine-deciduous habitat were probably the reasons for this difference. During midwinter, Tufted Titmice in areas supporting a heavy stand of Water Oak fed heavily upon the acorns of this species. Where Loblolly and Spruce Pine seeds were most readily obtainable, these food items predominated in the diet of the titmice. However, no stomachs of the titmice or the Carolina Chickadees in this area contained more than 85 per cent vegetable food, and few contained that much. Animal food was found in the stomachs of almost every chickadee and titmouse in the Longleaf Pine forest as well. This fact suggests that these species require a certain amount of animal food. In this area the chickadees did not apparently include Water Oak acorns in

their diet, though they fed heavily upon pine seeds where they were available. As a result, the food habits of the chickadees and titmice were much more similar when foraging in the area of a pine seed crop than when they fed in the oaks. In the oak areas, the chickadees ate correspondingly more heavily upon insect food.

SOME MISCELLANEOUS ASPECTS OF FLOCK BEHAVIOR

The size at which mixed insectivorous flocks can function with full effectiveness probably has definite limits. The size of flocks is dependent upon a number of factors, including the following:

1. Foraging preferences of the species
2. Behavioral characteristics of individuals such as hostility and joining actions
3. Characteristics of the habitat

When the size of a flock exceeds its limits of optimal effectiveness, an increase in hostile activity because of overcrowding often results. Species within a flock may reach a level of density where the individuals become so numerous that they cannot maintain an effective social hierarchy. If a spacing mechanism proves effective, the individuals spread out across the habitat so that cohesion decreases. With high numbers the food resources may eventually be inadequate.

Hinde (1952) distinguished two different types of flock movement, integrated and slow drifting. Integrated movements are largely unidirectional, independent of feeding, and usually of greater distance. Hinde felt

that they played an important part in keeping flocks of Great Tits together. When one bird gave a particular note and flew, others displayed a strong tendency to follow, their tendency to scatter during slow drifting movements thus being overcome. Slow drifting movements are largely the result of individual feeding activities and do not have as much tendency to be unidirectional as the organized ones. Both types were observed in all flocks in Maine and in Louisiana.

Speed is usually greater in large flocks (see Table XVIII), perhaps partly as a result of the increased possibility of performing following reactions. Brown-headed Nuthatches usually called distinctly before moving away from a flock, and often others of the same species soon followed. The particular call note given was similar to the one uttered when an individual became separated from the flock just as Hinde found in the case of the Great Tit. The tendency to produce loud notes preliminary to moving away from the flock was less pronounced in Black-capped Chickadees, though the loud notes given by separated birds were at times rather noticeable.

Different speeds of movement of individuals in a flock sometimes result in some individuals becoming separated from the main body of a flock. Species such as Downy Woodpeckers and Brown Creepers often lagged toward the rear of such flocks and could have become

dissociated more readily than some of the species remaining nearer the front of a group. However, both the Downy Woodpecker and the Brown Creeper showed a strong tendency to remain with the other species in the Louisiana flocks. When not utilizing pine seeds extensively, Brown-headed Nuthatches often moved faster in transit than the other members of the mixed flocks in the Longleaf Pines. This greater temporary speed sometimes resulted in their separation from the flocks. Fitch (1958) found that Golden-crowned Kinglets in mixed flocks in Kansas frequently moved away from Black-capped Chickadees in consequence of their greater foraging speed. My data as well as those of Odum (1942) indicate the opposite tendency; that is, the kinglets are more frequently left behind because of a slower rate of foraging. In England, Gibb (1960) found that the closely related Goldcrest also moved horizontally more slowly than the tits with which it associated. Fitch found that Black-capped Chickadees in Kansas foraged more rapidly than Tufted Titmice and that they sooner or later left the titmice behind. In Louisiana, where Carolina Chickadees and Tufted Titmice are territorial throughout the year often with widely overlapping or even quite similar territorial areas, no appreciable difference in foraging speed was noticed. As a result of their attracting influence on the other flock members, which was slightly

TABLE XVIII

MOVEMENT OF MIXED-SPECIES FLOCKS IN LOUISIANA (YARDS PER HOUR) DURING THE FALL AND WINTER OF 1964-65[1]

Size	Pine-deciduous[2]	Pine[3]
2-10	125 (2)	-
11-20	176 (6)	195 (4)
21-30	211 (4)	394 (5)
31-40	-	308 (6)
41-50	-	474 (2)

[1]The number of flocks is enclosed in parentheses.
[2]Satsuma study area.
[3]Fluker study area.

greater than that of the Carolina Chickadee, Tufted Titmice led the flocks more frequently than did the chickadees. In any case, Carolina Chickadees and Tufted Titmice, the two passive nuclear species observed to lead mixed flocks in Louisiana.

Gibb (1960) pointed out that the speed of English flocks was often partly dependent upon the presence or absence of Long-tailed Tits, which moved faster than any other species in those flocks. Long-tailed Tits occurred most frequently in the large flocks.

The fastest moving flocks in the Louisiana study areas were in the Longleaf Pine forest, the area where the largest flocks were also found. Gibb (1960) noted that flocks on English pine plantations consistently moved more rapidly than those studied in a broad-leaved forest. Hinde's work (1952) on Great Tits indicated that flock speed was much greater in the winter than in the late summer and fall. These facts suggest that the flock speed is partially correlated with the available forage.

Through mid-October, 1964, little or no suggestion of any organized flock movement existed in a mature deciduous forest south of Baton Rouge. Already by this time a suggestion of directional movement had appeared in the pine-deciduous area near Satsuma. By 28 October, noticeable directional flock movement was detected in

both of these areas. In the Longleaf Pine forest at Fluker, flocks were large and showed definite directional movement as early as 23 September.

Most organized flocks move in a definite direction, though the direction does change frequently and even results in backtracking at times. Seldom do the members of a mixed flock roam for any great distance. After a few hundred meters, Gibb's (1960) flocks of tits and Goldcrests usually turned and moved off in a different direction. As indicated in an earlier section of this paper, most (or all) mixed flocks regularly traverse a home range.

Mixed flocks seldom retrace previously used paths during their foraging. However, Stanford (1947) mentioned that the flocks he observed in Burma frequented certain bushes each time that they passed through areas under observation and that they ignored surrounding ones. In most cases, close study reveals that such flocks do not always move on identical paths, though first impressions may create the illusion that they tend to do so. Miller (1921) found that all cases in which definite paths were taken by flocks of Common Bushtits that he studied in California could be explained by preferences for particular types of vegetation. Beebe (1947) stated that tropical flocks that he studied in Venezuela seemed

to follow no definite routes. Working on Black-capped Chickadees, Butts (1931), Odum (1942), and Batts (1957) also indicated that no single set forage route was used. None of my observations indicate any distinct foraging pathways not related to foraging preferences, the ranges in question being fairly well-covered, except for parts that are apparently unsuitable for procuring food. At certain times of the year, however, the flocks in the Longleaf Pines showed a marked tendency to proceed along the edges of small streams, probably as a result of the seasonal foraging preferences of the passive nuclear species, the Carolina Chickadees and Tufted Titmice. Even Brown-headed Nuthatches and Pine Warblers, species that foraged almost exclusively in the pines, were affected by this seasonal behavior, though they worked principally in the pines adjacent to the stream edges.

The daily foraging schedule is subject to variation. A flock seen at one time in a certain part of its range will on other days appear there at different times, or not at all. Miller (1921) felt that the Common Bushtit flocks he observed moved on impulse, with the movement of a bird away from a forage place often prompting other birds to follow. This idea approximates the findings of Hinde (1952), discussed earlier. Odum (1942) found that Black-capped Chickadees do not appear to have definite leaders, but first follow one individual, then

another. Such a lack of organization as this results in an almost random foraging pattern.

When flocks move faster, the individuals show a stronger tendency to remain in one distinct favored part of the vegetation, the decrease in the width and height of the habitat investigated perhaps representing in the long run a more efficient means of foraging than random or prolonged search through many of the strata. Remaining in a narrow segment of the habitat reduces the number of encounters with other species. Members of large flocks display a definite tendency to forage in a narrow segment of the habitat in addition to moving faster. Examples from my field notes of 27 September 1964 in the Fluker Longleaf Pines are illustrative. Two flocks of 31 and 16 individuals, both containing the same number of Carolina Chickadees and Tufted Titmice, were observed. In each case, two pairs of chickadees were displaying where their territories overlapped or nearly apposed each other. A single pair of titmice were present during both territorial encounters. The larger flock moved approximately 340 yards per hour, while the smaller one moved approximately 150 yeard per hour. In the former case, the chickadees foraged largely on the smaller limbs in the upper part of the low oaks and also worked in the outer parts of the lowest pine limbs. Titmice spent a majority of their time in the larger parts of low pine

branches and larger limbs of the oaks. This flock tended to retain a constant movement in one direction. In the smaller flock, the chickadees exhibited a strong tendency to work in the low dense deciduous bushes, where present, in addition to the areas mentioned above. They also spent more time at greater heights in the pines and were more inclined to work nearer the trunk than in the first flock. The titmice also demonstrated a greater tendency to spend time in the dense deciduous area. The direction of movement showed more tendency to change in this flock than in the larger one.

A very small flock studied on 1 November 1964 exhibited the frequent foraging patterns of small flocks even more clearly. This flock consisted of only five individuals, two Carolina Chickadees, two Tufted Titmice, and one Brown Creeper. In this flock both the titmice and chickadees were first observed working in the lower oak growth. They then worked vertically at a slow rate and eventually reached a very high level in the pines, nearly at the top. The titmice as before appeared generally to utilize the larger parts of the branches, somewhat nearer to the trunk than the chickadees. The rate of advance of this flock did not exceed 112 yards per hour.

The size of flocks is extremely variable and is dependent upon the richness of the habitat, the season,

the number of potentially flocking species in a given area, and the interspecific and intraspecific tolerance of the forms involved. Some large flocks described by Hinde (1952) contained over 100 individuals, of which as many as 50 were Great Tits. After disappearance of the abundant beech mast food supply, the numbers diminished considerably. Distribution of food normally played a large part in determining the size of Hinde's flocks. My largest flocks contained between 40 and 50 individuals, excluding the ones containing large numbers of loosely associated Myrtle Warblers. Gibb (1960) found in his study of English pine plantations that the commonest flock size ranged between 10 and 20 birds, but that the majority of the flocking individuals were found in larger flocks. Chapin (1932) noted that some of this Congolese flocks contained as many as 40 to 50 individuals also.

Beebe (1917:104) observed one tropical flock of 28 individuals that contained 23 species. Many mixed tropical flock members avoid other individuals of their own species outside their immediate family (Skutch, 1954). On the other hand, some of the species that Moynihan (1962) studied in Panamanian mixed flocks were moderately gregarious intraspecifically.

The flocks that I studied in the temperate zone contained a maximum of 15 species, though usually considerably less. Many more species were present in the

late summer-fall flocks in Maine and in flocks in Louisiana than in the winter flocks in Maine, which contained the minimum number of species of any flocks studied.

Exceedingly large numbers of any single species in a mixed flock are a disruptive factor, and none of the most strongly flocking birds in my studies were found in large numbers within a restricted area.

In studies of Black-capped Chickadees, Hamerstrom (1942) gained the impression that the number of chickadees in a flock has more influence on the amount of fighting than the weather. Odum (1942) observed a greater tendency in the Black-capped Chickadee at times of high density for the number of flocks to increase than for the number of individuals per flock to increase. Both Hamerstrom and Odum noted social hierarchies in this species. Davis (1946) noted in Brazil that although the number of flocks, the number of individuals, and number of species in each flock might vary, that any species present in a flock was represented by about the same number of individuals, regardless of the season. Wallace (1941) indicated that a normal-sized flock of Black-capped Chickadees in Massachusetts included six to eight individuals. Whittle and Fletcher (1924) gave similar figures for another part of the same state.

The 29 different flocks that I counted during February and March, 1957, in Androscoggin County, Maine,

demonstrated considerable variation in flock size but contained a maximum of 12 Black-capped Chickadees and yielded an average comparable to the figures given by Whittle and Fletcher and Wallace (see Table XIX). In addition, smaller numbers of Red-breasted Nuthatches and Golden-crowned Kinglets accompanied the chickadees.

During late December, 1964, the largest flock observed in this same area also contained 12 Black-capped Chickadees. A noticeably greater amount of hostile behavior was exhibited in this flock than in any of the smaller flocks, none of which contained over eight chickadees. Some of these smaller flocks were studied on the same day as the large flock. Though the hostility consisted primarily of supplanting attacks, one or more actual fights occurred in which bodily contact was observed. Collias (1944) stated that more fighting probably occurs in large groups than in smaller ones, and that it takes longer for a social hierarchy to become stabilized in such a group than in smaller groups.

A similar situation to that described for the Black-capped Chickadee may exist in Brown-headed Nuthatch flocks. Seldom were more than ten individuals of this species observed together. All these data suggest that the maximum number of individuals of a species that can effectively utilize an area is rather low.

In Maine, when the warblers are just past the breeding season, and when some reproductive behavior may still remain, much hostile behavior is exhibited. The high population resulting from the many young just produced by the warblers and other species, is compounded by the addition of migrants. In some species because of the high population and constant change of members, a completely stable hierarchy cannot develop. Further hostile behavioral patterns in these species may be heightened by their close relationship and consequent similar foraging and feeding behavior. This high density probably produces the same result when the permanent residents attain an abnormally high population, and the increased hostile behavior will aid in dispersing the individuals. Such a series of developments might provide a behavioral stimulus encouraging migration (see Wynne-Edwards, 1962:418).

Collias (1944) noted that after a certain density was reached, aggressive behavior appeared to decrease, perhaps because new members could no longer be recognized. I did not observe an outcome of this sort in any winter flocks, probably because the food sources in the study areas would not support an extremely high population for any length of time. One might expect such a phenomenon to be more prevalent among species that have definite nomadic tendencies and which exploit

TABLE XIX

FREQUENCY OF BLACK-CAPPED CHICKADEE FLOCKS OF VARIOUS SIZES OBSERVED IN ANDROSCOGGIN COUNTY, MAINE, DURING FEBRUARY AND EARLY MARCH, 1957

Number of chickadees in flock[1]	Number of flocks
1	1
2	0
3	0
4	3
5	2
6	5
7	3
8	7
9	3
10	3
11	1
12	1

[1]Average of 7.2 chickadees per flock.

temporary food wources. Flocks of cone-feeding fringillids and frugivorous flocks would fall into this category.

In Louisiana in winter, Myrtle Warblers are frequently found with mixed flocks and also occur independently of them. Usually the large groups of Myrtle Warblers associated with the mixed flocks are extremely restless, move rapidly, and break away readily.

On 16 November 1963 a group of about 50 Myrtle Warblers in a mixed flock at Satsuma moved rapidly through the pine-mixed deciduous foliage with the members distributed from nearly ground level in the thick young Loblolly Pines and deciduous thickets to the treetop foliage, which approached 100 feet in height in the case of the largest pines. Similar behavior was observed at Fluker in the Longleaf Pine forest, though the vegetational complexity here was not sufficient to provide as striking an example as the one at Satsuma. At Fluker, these members of large groups were distributed from the lower deciduous growth to the pine tops, 50 or more feet high.

Probably this diffusion is due to the sheer numbers of Myrtle Warblers alone, and because of the aggressive intraspecific nature of these birds it is probably a critical factor. This diffusion exposes some of the Myrtle Warblers to foraging conditions sub-optimal for

this species, occasioning faster foraging and an increased tendency for parts of the group to fragment off and become separated. The urge to follow in this species appears so strong that it may even induce all the Myrtle Warblers to leave the mixed flock en masse. Single Myrtle Warblers or even small groups of them remain much closer to mixed flocks than do the larger groups. In addition to increasing intraspecific fights and suboptimal foraging, large numbers heighten contact with other species of the mixed flocks, particularly in the parts of the habitat that the Myrtles do not otherwise frequent. Undoubtedly the presence of Myrtle Warblers in large numbers enhances hostile behavior in all species involved.

Semi-nomadic species such as the Myrtle Warbler do not regulate their numbers in an area in the same manner as do the Black-capped Chickadees; however, they become more mobile as their density increases, and they often emigrate, thus lowering density or at least discovering an area with an adequate food supply. This mechanism has the disadvantage that it brings the birds into foraging areas with which they are not familiar, though in Louisiana they usually are able to find at least a temporary vegetable food source. One of the more prominent species in the vegetation of the sparse and scattered understory of the Longleaf Pine forests is the

Waxmyrtle (Myrica cerifera), a species producing berries frequently fed upon by the Myrtle Warbler. In addition to the mass movements, single Myrtle Warblers or small groups of them were frequently seen flying over the study areas during the winter season, giving some additional idea of their wandering tendencies in this region.

Permanent residents face more restricted alternatives, as they do not move freely in such a manner. Their sedentary habits partly explain why permanent residents often utilize territoriality or maintain some sort of social hierarchy such as that seen in the Black-capped Chickadee.

On 4 January 1965, a large flock including over 20 Pine Warblers was seen in the Longleaf Pine forest at Fluker. In contrast with their behavior when in smaller numbers, these birds acted in a manner suggestive of large flocks of Myrtle Warblers. Normally aggressive, the birds became even more so, with a resultant increase in interspecific fighting. A change in the foraging pattern was also noticeable. Trunk foraging, a regular habit of Pine Warblers, increased markedly, and the amount of foraging performed on the ground and in the low deciduous growth was unprecedented. I had previously made few observations of Pine Warblers foraging in coniferous growth at Fluker during the period of the study, but at this time a substantial percentage of the birds, at

times probably as great as 25 per cent, were foraging either on the ground in the sparse grass and weed cover or in the low deciduous understory, composed primarily of Blackjack Oaks. These birds moved rapidly and showed a strong tendency to follow other Pine Warblers that had flown ahead. Usually Pine Warblers follow Carolina Chickadees and Tufted Titmice very closely, but under these circumstances the warblers had a stronger tendency to follow other members of their own species than to be led by the chickadees or titmice. They moved so rapidly that they eventually broke away and moved off on their own.

Winter mixed flocks in Maine moved even more rapidly than the Louisiana pineland flocks. Fewer species were found in these flocks, perhaps because of the rigorous environmental conditions. With fewer species, each form has access to a wider section of the habitat, and one might expect a slower rate of foraging to result. If more flocking individuals of more species had been present in the conditions then existing the flock might have moved even more rapidly. During one period of observation in late December, 1964, Black-capped Chickadees were feeding rather heavily upon a moderate supply of Balsam Fir (Abies balsamea)cones. In spite of the concentrated food source, they did not linger long over any one cone or tree, but usually after cracking no

more than two or three seeds they would immediately continue on. Large flocks appeared to move more rapidly than small ones.

FACTORS FACILITATING GREGARIOUSNESS

Many birds possess characteristics that facilitate gregariousness. These include a dull plumage, a low level of hostility, possession of notes that attract, and repression or absence of distinctive song.

Vocalizations appear to play a central role in the promotion and maintenance of flocking. Most flock members, particularly the nuclear elements, are vociferous. An active flock is indeed a conspicuous entity. Notes uttered in flocks do not include all the vocalizations that a species possesses. Singing rarely occurs in a highly organized flock.

Moynihan (1962) pointed out that tropical passive nuclear flock members such as Palm Tanagers, Plain-colored Tanagers, Blue Tanagers, and bush-tanagers are nearly constantly vocal. Their noise attracts many other species. In some species, including Blue Tanagers and bush-tanagers, song is reduced and is quite similar to the chattering notes given in the flock. Chapin (1932) noted that none of the birds in the forest flocks that he observed in the Congo were especially good singers and that the notes in these groups were mostly of a

twittering or chirping nature. Call notes may be very important in maintaining contact with other flock members, particularly in growth so thick that visual contact is difficult to maintain. In British Honduras Willis (1960b) found that Red-crowned Ant-tanagers possessed less elaborate songs than did Red-throated Ant-tanagers. Red-crowned Ant-tanagers (Willis, 1960a) were found in mixed foraging flocks much more frequently than were the Red-throated Ant-tanagers.

Temperate flock members that I studied are not as conspicuously vocal as Palm Tanagers, Blue Tanagers, and bush-tanagers; but many do utter location notes almost constantly. The hostile territorial defense notes of the Tufted Titmouse and Carolina Chickadee are frequently uttered, are very conspicuous, and attract other species very strongly, instead of having little effect as might be the case if the song were utilized. These calls often effectively increase flock cohesion. Probably few species have aggressive notes that attract other species as strongly as these two. The difference in the interspecific reaction to hostile call notes on the one hand and song on the other can be observed in the spring when the chickadees and titmice are singing regularly, usually away from the flocks.

Some of the more strongly flocking species have an extensive repertoire, or at least put certain parts of it

to extensive use. As a result, a greater amount of information can be conveyed than is possible in other species. Odum (1942) listed 16 different vocalizations for the Black-capped Chickadee. Carolina Chickadees possess a comparable repertoire (see Brewer, 1961) and that of the Tufted Titmouse appears as various. The use of similar or superficially similar vocal patterns under conspicuously different conditions may result in different reactions.

During the winter in the nonterritorial Black-capped Chickadee its variety of vocalizations probably aids in minimizing energy-consuming aggressive behavior (largely intraspecific), making it possible for the individual to expend more energy and time in other activities, particularly in the search for food. Supplanting attacks are the usual limit of aggressive behavior in winter flocks of Black-capped Chickadees. These attacks are a less disruptive element in the flock than contact encounters. Also, the members involved can maintain a much greater alertness and remain less subject to predation than if frequently fighting. Even in territorial Carolina Chickadees and Tufted Titmice, vocalization represents the most conspicuous element of aggressive behavior.

Not all flocking species possess such a wide variety of vocalizations, and in some of these, a much higher

level of hostile behavior occurs. The Pine Warbler is largely silent when in flocks and indulges in many elaborate spiralling aerial fights, especially with other individuals of its own species. In addition, it is often rather aggressive in its relations with other flock members.

A number of species that are loose associates of the flock sometimes follow along locally and frequently contribute their vocalizations to the general noise of the flock. Their notes add to the total variety of flock sounds and might therefore make the entire flock attract a wider range of species than would otherwise be the case. Moynihan (1962) felt that the presence of a large variety of sounds might have caused his tropical flocks to attract more species than they could otherwise and even suggested that the notes of a squirrel scolding (probably Sciurus granatensis) might enhance the effect.

Some species, including passive nuclear species, appear attracted to only a relatively few notes or combinations of notes and other stimuli. Carolina Wrens are a common species in several of the study areas. They are extremely vociferous, and at a first glance it appears that their notes would be a very attractive stimulus to other species, particularly their rasping scold note, which sounds superficially like a vigorous scratchy Tufted Titmouse scold note. Only infrequently

do other species show signs of being attracted to this species. As previously mentioned, most flock species respond excitedly to the aggressive notes of both the Tufted Titmouse and Carolina Chickadee. Thus, these flocking species hav learned to distinguish between quite similar patterned notes. Carolina Wrens frequently sing when flocks are present; they also remain in the underbrush and do not move for appreciable distances, being quite strongly territorial.

On the other hand some of the Black-capped Chickadees that I studied in the summer in Maine showed a tendency to respond to a rather wide variety of notes, including the sounds of young begging Brown-headed Cowbirds. Such behavior has no discernible selective value, though at this season there probably is little selection against a moderate amount of such behavior. Many of the chickadees showing flocking responses at this time have been demonstrated by Odum (1941b) to be young birds; this fact may indicate that disregarding such a stimulus is learned behavior.

It would be of importance at times of severe environmental conditions to react only to those notes that will be of effective use. Responses such as the one to the cowbird are not beneficial to the bird's energy balance. At some times of the year it may be of importance to carefully regulate energy stores, and every

squeaking tree might present a formidable problem for flocking birds if they readily responded to it. The fact that human observers often can attract Black-capped Chickadee flocks only a limited number of times by "squeaking" or "shushing" is an indication that learned behavior is involved and that it may be rather effective.

Some notes of similar sound given by different species may serve an interspecific function. The notes most frequently similar are those that the birds use primarily for location purposes while in flocks. They probably are of considerable importance in keeping the members of mixed flocks in close contact with each other. Notes of many warblers in the fall, ranging from the Black-and-White Warbler to the American Redstart, are so similar that the human ear cannot differentiate between them. Even the location note given by the Black-capped Chickadee bears considerable resemblance to those of many warblers. The location notes of Brown Creepers and Golden-crowned Kinglets are so similar that it is difficult for the human ear to detect a difference. Others are readily distinguishable, as in the case of the nuthatches, Ruby-crowned Kinglet, and others. Even in these cases the location notes consist of single notes or short series of notes, usually of low volume, that are much more similar to those of other species than to the remainder of the emitter's repertoire.

When individuals are separated from flocks, many of them give loud notes that are distinct form the usual location notes and usually elicit a similar vocalization from other individuals, at least those of the same species. These notes are more species-distinct than the regular location notes and often are among the more familiar calls of a species, functioning in other ways under different circumstances. Chick-a-dee notes are used in this manner by the Black-capped Chickadee, as are loud yank-yank-yank notes by the Red-breasted Nuthatch and see-see-see notes by the Brown-headed Nuthatch.

The warbler calls heard in the fall flocks are not given before late summer, when the breeding season is ending and territoriality is waning. In the breeding season a premium against such notes probably exists, as notes that might not be distinguished as species-specific could prove detrimental to the maintenance of reproductive separation between species in the breeding season. As it is, considerable hostile behavior is exhibited among warblers in flocks in the late summer and fall, but such factors as a similarity of notes may prevent an even greater incidence of hostility.

I have observed migrant fall warblers descending from the dawn sky, presumably landing in a particular place as a result of answers to their calls given by other individuals in the trees. On Hog Island, migrant

warblers frequently were seen to alight just before sunrise and loud call notes of warblers were scattered throughout the area. Soon the birds joined the Black-capped Chickadee flocks and became quite silent. This phenomenon was also noted by Odum (1942).

A considerable tendency exists for the nuclear members of a flock to be of a neutral or dull hue. Such color combinations would probably prove less antagonistic than bright ones (Moynihan, 1962).

With respect to their evolution one might ask whether these birds became flockers after acquisition of such a plumage; or, whether being flockers, they later attained this plumage. Some of the tropical tanagers may throw light on this problem.

Palm Tanagers, Blue Tanagers, Plain-colored Tanagers, and bush-tanagers come from a family noted for its colorful appearance. The genus Tangara, which includes the Plain-colored Tanager, consists mostly of very brightly colored birds, and includes some of the most colorful birds in the world. Thraupis, which includes the Palm Tanager and the Blue Tanager, is for the most part a moderately bright genus, and Chlorospingus, which includes the bush-tanagers, consists of a number of quite similar dull species. The species named above are all either of relatively dull or neutral hue (see Moynihan, 1962).

Some other species of dull tanagers flock, including the Tawny-crested Tanager and the Olive Tanager. In several sexually dimorphic species, for example the Scarlet-rumped Tanager, the females and dull young flock more strongly than the bright males (Skutch, 1954). The Scarlet-rumped Tanager is a sexually dimorphic species that is noticeably vociferous. The bright males possess a prominent flash pattern that may be a very antagonistic character. I found this species to be loud and quarrelsome during my studies in Costa Rica. Any flocks that are formed about this species are of limited composition and stability, probably because of the aggressive behavior presented.

A high percentage of top and edge species of the tropical forest are very bright; birds of the dense forest below the treetops are frequently dull. This distribution is merely a generality; exceptions can be found. Such species as the Palm Tanager, Blue Tanager, Plain-colored Tanager, and Sooty-capped Bush-tanager are birds of the forest edge and bush, yet they are dull or of a neutral hue. However, these birds are not as inconspicuous as some of the green foliage-inhabiting species, including the Rufous-winged Tanager and Bay-headed Tanager. The dull plumage of the previously-mentioned tanagers probably is not an adaptation for concealment (see Moynihan, 1960). The Common Bush-tanager, which is

closely similar to the Sooty-capped Bush-tanager, is often a denizen of the heavy forests. All these birds share the characteristics of being extremely and continually vociferous, of being dull, and tending strongly to flock.

Many of the warblers don a dull fall plumage, this being worn at the time that their participation in mixed flocks is at a maximum. The suggestion of Hamilton and Barth (1962) that this is an adaptation to avoid intraspecific inter-individual hostility in gregarious situations, such as occur in migratory and winter flocks, may have considerable merit. In addition, this factor may also function interspecifically, the plumage of the different species after molt becoming much more similar to each other than they were during the breeding season. When one considers the elaborate mechanisms that exist serving to isolate some of these species in the breeding season (see MacArthur, 1958), it becomes evident that if this separation were maintained, it would be impossible for these species to make maximum use of the great food potential existing in many areas adjoining the nesting grounds.

THE ROLE OF MIGRANTS IN MIXED FLOCKS

Though I have earlier questioned the importance of predator protection as a benefit of flocking, nonmigrant foraging flocks including migrants may be of greater aid to the migrant in protection from predation than to the permanent flock members. Since migrants probably would wander randomly over a strange habitat if they did not join flocks, their presence in a flock might lessen their vulnerability to predators. Away from flocks they would be even more subject to depredation than when in flocks, simply because of their unfamiliarity with the terrain. In addition, they may not be in top physical condition if they have just made a long migratory flight. I have indicated elsewhere in this paper that mixed flocks concentrate in areas of heavy insect infestations during the late summer and fall. Being drawn into such a group will enable migrants to take advantage of an abundant food source. However, if the density of other birds is high, the migrant will experience considerable hostile behavior from the flock members, particularly if it is a close competitor of any of the others. The migrants are often relegated to the bottom

of the social hierarchy, which will be a disadvantageous position if competition is heavy. Migrants seldom play a significant part in the social behavior of a flock. A high level of hostile behavior on the part of regular flock members may act as a cue that will enhance the tendencies of migrants to continue their movement (see Wynne-Edwards, 1962:418).

REGULATION OF POPULATION DENSITY AND THE FOOD SUPPLY

Wynne-Edwards (1962:417) has introduced the interesting idea that mixed bird flocks perform an epideictic function. He defines an epideictic phenomenon as a symbolic display, which gives the individual an adequate indication of the population density of its species (and other species). By appropriate actions members of the population can then adjust density to suit the carrying capacity of the habitat. A synchronized chorus of frogs or the above-mentioned mixed flocks of birds serve as examples. Epideictic displays usually do not involve direct contests that could involve bloodshed or even the death of a participant. They thus represent a more efficient means of density regulation than direct combat or widespread starvation.

In the flocks that I studied it was apparent that increased hostile behavior occurred in flocks containing an unusually large number of individuals of a species. The mere presence of abnormally high numbers of individuals in a flock is apparently in itself not sufficient to set the mechanism hypothesized by Wynne-Edwards in action.

In mixed flocks of birds the problem of the conservation of an adequate food supply through a period of minimum supply may be the most important aspect of the regulation of a population. Epideictic phenomena, as defined by Wynne-Edwards, represent a more efficient method of keeping a population within bounds than methods necessitating less organization. However, though several adaptations toward more efficient flock feeding have been described in this paper, it must be noted that flock foraging by no means represents the most effective manner in which a bird can hypothetically obtain food from an environment. An individual could obtain much more food by foraging in a limited area than it could by keeping up the characteristic rapid movement of the flocks. Only a small percentage of readily obtainable food in an area is probably removed by a bird (or by a flock) each time that the flock passes through. Rapid movement burns up much energy that is badly needed at times by the birds. Though hostile behavior appears less prevalent in flocking species than in nonflockers, some energy is used up in this manner. While it is doubtless true that any species forages most effectively in one certain part of the habitat and that this segment is one certain area usually exploited most heavily while an individual is participating in a flock, the individual probably could obtain more food and expend less

energy by foraging in a wider part of the habitat and avoiding the inevitable onward rush of the flock.

In areas where food sources are not constantly replenished, some conservation of this supply may be necessary to insure that an adequate amount is saved to tide the individuals over until replenishment occurs. An example of this problem occurs in northern forests, which become essentially dormant during the winter except for the activity of warm-blooded vertebrates. The food supply that exists in November is the one that must last through the winter. Here insects do not produce young at this season; they probably do not even move until spring. If the food supply did not last through the winter an individual would be faced with the necessity of either emigration or starving. This problem becomes extremely critical in the cases of species that do not exhibit appreciable migratory tendencies.

Two alternatives lie in territoriality and flocking. By defending an area of adequate size an individual may insure that an adequate food supply will remain for the winter. Territoriality appears to be effectively utilized at this season by some species including the Carolina Wren and Mockingbird in Louisiana. Other species in this state participate frequently in flocks, though remaining territorial. These include Carolina Chickadees and Tufted Titmice.

Under severe environmental conditions, flocking appears more prevalent than under less severe ones. Hinde (1952) indicates that some species of English tits give up a territory and join flocks when environmental conditions become harsh. Carolina Chickadees show less tendency to defend a territory along the northern limits of their range than they do in southeastern Louisiana.

Some species of birds, such as the Black-capped Chickadee, show an extremely strong tendency to be found in a flock and during the seasons that such groupings are in existence are seldom found away from them. By participating in flocks birds reduce the amount of fighting that is associated with the defense of a territory. The presence of a social hierarchy will contribute substantially toward lowering this level. More time can then be devoted to other activities, though at least part of this time will be taken up in rapid directional movements.

Most likely rapid movements are the result of individuals in a flock following other members. The speed of a flock increases directly with its size. When flocks are large more individuals are present to fly away from the flock and be followed by other flock members. However, the individuals being followed are usually passive nuclear species. In Louisiana, where the passive nuclear species are territorial and thus not in great

numbers, large flocks still move faster than small ones. Hence, the possibility that escape reactions on the part of the passive nuclear species are at least partly involved should not be ignored.

Since large flocks move faster than small ones, they spend more time and energy in flock movement than do small ones. The available feeding time is decreased, and this curtailment may be a force serving to keep them from growing subsequently larger.

As a result of the attraction of a flock, a large percentage of heavily competing insectivorous species in an area may be found within it. This grouping may function in conserving the food supply of the environment by regulating the number of individuals within this environment.

When the individuals of a species in a flock surpass an optimal point, hostile behavior increases, which will serve to reduce the number of this species. Increased close contact with strongly competing species will result in an increase in hostile behavior between such species. This behavior contributes toward the interspecific control of the population.

The presence of a superabundant food supply of Longleaf Pine seeds resulted in a somewhat reduced tendency for Brown-headed Nuthatches to be found in mixed flocks. The birds were not faced with the problem of maintaining

a food supply, the stable one of animal food at that time.

Under tropical conditions, food may also be a critical factor, as in most areas where flocks have been studied, wet and dry seasons alternate, and the result is a variation of the food supply. Wherever a fluctuation in food supply occurs, flocking could be of benefit to keep population density in line with the period of minimum supply. In addition, some tropical flocks are swelled in numbers seasonally by the addition of northern wintering species. This influx partially coincides with times of minimum food supply.

Most members of mixed flocks have food habits that overlap to a considerable degree. Moynihan (1962) noted this condition in the mixed tanager and honeycreeper flocks that he studied in Panama. Such is definitely the situation in all flocks that I have studied. The species involved are in competition to varying degrees and the more frequently species overlap widely in food habits, the more restrictions are placed upon the population of a given species. The greater the overlap, the fewer individuals of the species concerned that can be accommodated. Though the food supply in the tropics may be richer, the shortages may still exist, because of the profusion of birds. Food may appear in abundance most of the year, but some factor must keep numbers in

check. If the ultimate factor is food, then the period of minimum supply is critical, and there would be selection for individuals that possessed some means of regulating the numbers to fit the food supply. This method might effectively be accomplished in a mixed flock.

FUNCTION OF FLOCKING

Many functions have been ascribed to flocks, including beating for food, protection from predators, an improved method of foraging, efficient division of habitat, and regulation of population density and food supply.

In addition, some earlier investigators also concluded that flocking served the purpose of satisfying an inherent sense of gregariousness present in the flock members. This appears self-evident and the field observations I have made support such a statement. As Colquhoun and Morley (1943) state, the psychological attraction of a flock to its members cannot be denied. However, as Moynihan (1962) points out:

> The development of a gregarious instinct that can be satisfied by association in mixed flocks is probably a means to an end, not an end in itself. .... Such instincts probably have been evolved, in all or most cases, because interspecific gregariousness provides certain concrete advantages.

On the basis of this quote further explanations for the function of flocks may be sought, though the possibility does exist that the habit is presently of little or no advantage.

Summer flocks in the study area in Maine were basically foraging groups, although the rate of feeding was not as rapid as in winter flocks. Though flocks were more frequent in the birches, the area containing the most food and highest population density, than in the surrounding spruce forest, the source of food there was temporary and superabundant. Local birds could readily partake of these resources without undertaking extensive movements. In addition to the summer residents, migrants swelled the numbers. The latter two categories of birds would not remain during the winter. Thus, this density situation is not comparable to that existing in the Louisiana study areas in winter, where the largest and most highly organized flocks occur in the area supporting the lowest density, the Longleaf Pine forests. The birds located there are present during the periods of minimum food abundance. The temporary members in Maine flocks are present only at a time of high food abundance.

The winter flocks in both Maine and Louisiana spent almost all their time foraging. In the Louisiana study areas they made up a greater percentage of the bird population in the area (Longleaf Pine forest) supporting the lowest density. These flocks were larger and more highly integrated in this area and some species showed a stronger tendency to be found in flocks in this area

than in any of the other areas studied. In the fall, foraging in the flocks in Louisiana was more leisurely than in winter, with little directional flock movement being observed in the richer foraging areas.

Tropical flocks may spend less of their time foraging than do resident winter species in the temperate zone, and some tropical flock activities do not appear to be related to feeding (see Moynihan, 1962). At the times that I have observed nonaggressive flock behavior not related to foraging in the temperate flock members, individuals have upon occasion interrupted this activity and fed successfully. I have witnessed this phenomenon during the process of joining actions, such as when a Magnolia Warbler was observed approaching a Black-capped Chickadee, probably in response to some of the chickadee's activities. The warbler interrupted this movement to feed upon an object of food, which it apparently had just discovered in its movement toward the chickadee. Evidence is lacking to indicate that the temperate flocks I studied have a more important social function than as foraging groups. When feeding activity declines, there is a definite tendency for these groups to dissipate somewhat.

The above statements are not intended to imply that these are the only benefits to be obtained from flocking. The presence of a predator alarm mechanism in many flocks

makes it impossible to dismiss completely a protective function from the advantages of flocking, though available evidence from flocks that I studied indicates that it is of limited use in these groups.

In summation, mixed flocks may serve a variety of functions, the importance of each being subject to modification depending upon the characteristics of the area foraged and the species involved. In the temperate zone flocks that I studied intensively, the most important apparent advantage was a foraging one. Population regulation may be an important function, though further work is necessary to elucidate how this phenomenon operates in mixed flocks.

ORIGIN OF FLOCKING

The purpose of this paper is not to present a detailed discussion on the presumed origin of mixed-species flocks. One can find treatments of the subject in Stresemann (1917), Friedmann (1935), and Moynihan (1962). I shall simply attempt to make a few brief comments on this topic based upon my personal work.

Moynihan (1962) presents a hypothetical model of how flocks may have originated. His thesis is that the first stage in the evolution of flocks occurred when bonds were formed between a species that was intraspecifically gregarious and one that was not, and the one that was intraspecifically gregarious became in almost every instance the passive nuclear species.

In the Louisiana flocks passive nuclear species are not gregarious. Carolina Chickadees and Tufted Titmice are the passive nuclear species, but remain definitely territorial. The only species occurring in moderate or large numbers in Louisiana flocks are active nuclear members or attendants, such as Brown-headed Nuthatches, Golden-crowned Kinglets, Myrtle Warblers, and Pine Warblers. However, to the north Carolina Chickadees and

Tufted Titmice show a greater tendency to be intraspecifically gregarious. Many other parid species are strongly gregarious, though the family ranges from interspecific gregariousness to the maintenance of solitary pairs for the span of an entire year.

The Black-capped Chickadee is a passive nuclear flock member that is intraspecifically gregarious and the contrast of its behavior and that of the southern Carolina Chickadees illustrates how different the habits of two closely related species may be. Variation in gregariousness even exists between northern and southern populations of Carolina Chickadees. The situation with the chickadees reveals one of two possible conditions; either the flocking habit was retained grom gregarious ancestors in the case of southern Carolina Chickadees or flocks may be readily evolved and develop in different ways.

Davis (1946) felt that flocks have evolved independently in many different areas. The variety of the taxonomic groups participating as mixed flock members in different geographical areas is too great to permit placing a strong phylogenetic value upon this trait. More likely, the joining of birds into mixed species flocks represents an efficient adaptation of a mixed population to the environment.

SUMMARY AND CONCLUSIONS

A study has been made of the behavior and ecology of selected mixed foraging flocks of birds in Louisiana, Maine, and Costa Rica. Other aspects of mixed flocks have been considered in less detail.

Information gathered indicates that protection from predation often is not a factor of great advantage in mixed flocks. Alarm notes may offset the apparent disadvantage of increased conspicuousness of concentrations of birds. Many flocking species possess such notes and subsequent defense actions that doubtless would not have evolved unless they possessed selective value. Alarm responses appear relatively ineffectual with respect to some members of mixed flocks. False alarms are not infrequently given.

The tendency for a territory to be given up outside of the breeding season is greater in severe environments than in less severe ones. In Louisiana, Carolina Chickadees and Tufted Titmice have a strong tendency to defend a territory throughout the winter. From south to north there is an increased tendency for the same two species to relinquish a territory during the winter.

When a species is territorial, its foraging range is often comparatively small. If this territorial species is a flock leader, flock movement of associated nonterritorial species may be restricted unless contact is made with another flock.

A number of characteristics observed in different winter populations of birds in Louisiana indicate that flocking facilitates a satisfactory energy balance for the individuals involved. In the area supporting the lowest density of birds I found the largest flocks, the greatest spacing between flocks, and a greater tendency for strongly flocking species to be closely associated with flocks than elsewhere. Other factors, including weather and season, modify the tendency for birds to join flocks.

Seldom do birds largely restricted to the ground stratum form a conspicuous part of the flocks. Birds frequenting almost any vegetational level may occur in mixed flocks, except for those that cling strongly to the ground and underbrush. Individuals are seldom widely separated in height from all other flock members.

Many closely related species found together in mixed flocks possess complementary feeding patterns. Such a condition is demonstrated by Carolina Chickadees and Tufted Titmice in Louisiana. In both the Black-capped Chickadees and Carolina Chickadees studied by Brewer

(1963) in Illinois, patterns of foraging are very similar to those of the Carolina Chickadees in Louisiana, but rather different from comparable data on Black-capped Chickadees in Maine. This difference suggests that Black-capped Chickadees in Maine are occupying essentially the same foraging position as the one occupied by the Carolina Chickadees and Tufted Titmice combined in Illinois and in Louisiana. The wider foraging range of the Maine birds within their habitat may be the result of absence of close competitors. The chickadees in Maine showed a greater tendency to alter their habits to varying food supplies than did either species of parid in Louisiana.

Where complementary foraging patterns do not exist among closely related species, considerable hostility may occur. Golden-crowned and Ruby-crowned Kinglets forage rather similarly and much antagonistic behavior occurs when they come together during the wintertime. In the winter season these two species are often only narrowly sympatric.

Temporary flock members found in flocks studied in Maine during the late summer and fall, mostly warblers, also possess a high level of hostile activity. Many species with rather similar foraging patterns are present, and remnants of breeding behavior still exist.

In Louisiana, the foraging patterns of Brown-headed Nuthatches in and out of mixed flocks differ strikingly, this difference appearing to be largely the result of the presence of Pine Warblers in most mixed flocks. Probably the foraging behavior of Pine Warblers in mixed flocks is somewhat modified by the presence of Brown-headed Nuthatches.

A superabundant food source often results in a noticeable change of foraging behavior, though hostile behavior remains and may even increase. This phenomenon is likely the result of an increase in interspecific contact. During the period of an abundant source of Longleaf Pine seeds, a number of species fed heavily upon them. Brown-headed Nuthatches were the most dependent upon this source of food and had to change their spatial position in order to crack the seeds in parts of the tree containing suitable crevices. Some species, particularly the Brown-headed Nuthatches, showed a somewhat reduced tendency to participate in flocks during the period of seed abundance.

Stomach analyses generally coincided with foraging observations, though during the abundance of pine seeds more apparent foraging in the foliage, on the limbs, and on the trunks was observed in several species than might have been expected by the predominance of pine seeds in the stomachs. A wide variation in food items

from one closely situated locality to another was also indicated.

Most individuals in mixed woodland flocks have a considerably greater ability to retrieve food that they have flushed or dropped than usually attributed to them, thus lessening the possible flocking advantage of capturing food flushed by other members.

The speed of advance of flocks tends to vary directly with the number of individuals in a flock, and probably is modified by a number of factors, including the season and the species present in the flock. Mixed flocks seldom move over fixed routes. These groups are almost always local, the members being situated on a home range or a territorial space. Territorial members show a greater tendency to drop out of a flock than nonterritorial members in the flocks studied. In larger flocks, birds usually forage through a narrower part of the habitat, and thus may minimize contact with other species as well as concentrate on the stratum that they exploit most efficiently.

Some flocking species display a strong tendency to limit their number within a flock. Regulation is probably accomplished largely by the modification of hostile activities in response to the size of the population. Such a control of numbers may be a major benefit arising from flocking, though this hypothesis demands further

investigation. Other species reach high densities within flocks but do show a strong tendency to leave the flock under these circumstances. None of the most integrated mixed flock species attain very high densities in flocks. Among those species that do reach these levels, the Myrtle Warbler has nomadic tendencies. Nomadic flocks might be the most efficient means of capitalizing on scattered, sporadic abundant food sources such as cones or fruit.

Many flocking species possess characteristics that are probably of benefit to them as flock members. These include dull plumage, a low level of hostility, possession of notes that attract, and repression of distinctive song.

Flocking species respond to a number of different notes, but they are selective in their choice. Selection would work against response to extraneous signals at times of maximum energy demand.

Flocks may have evolved in a number of ways. The diversity of species flocking in different geographical areas, and the variety of behavioral conditions existing suggest that mixed flocks have little phylogenetic basis, but more likely represent an efficient adaptation of a mixed population to the environment.

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APPENDIX

SCIENTIFIC NAMES OF SPECIES OF BIRDS REFERRED TO IN TEXT

Double-crested Cormorant	*Phalacrocorax auritus*
Great Blue Heron	*Ardea herodias*
Turkey Vulture	*Cathartes aura*
Black Vulture	*Coragyps atratus*
Sharp-shinned Hawk	*Accipiter striatus*
European Sparrow Hawk	*Accipiter nisus*
Cooper's Hawk	*Accipiter cooperii*
Red-tailed Hawk	*Buteo jamaicensis*
American Sparrow Hawk	*Falco sparverius*
Bobwhite	*Colinus virginianus*
Great Black-backed Gull	*Larus marinus*
Herring Gull	*Larus argentatus*
Wood Pigeon	*Columba palumnis*
Mourning Dove	*Zenaidura macroura*
Black-billed Cuckoo	*Coccyzus erythropthalmus*
Yellow-shafted Flicker	*Colaptes auratus*
Pileated Woodpecker	*Dryocopus pileatus*
Red-bellied Woodpecker	*Centurus carolinus*
Red-headed Woodpecker	*Melanerpes erythrocephalus*
Yellow-bellied Sapsucker	*Sphyrapicus varius*
Cardinal Woodpecker	*Dendropicus fuscescens*
Hairy Woodpecker	*Dendrocopos villosus*
Downy Woodpecker	*Dendrocopos pubescens*
Red-cockaded Woodpecker	*Dendrocopos borealis*
Eastern Phoebe	*Sayornis phoebe*
Drongo	*Dicrurus* sp.
Blue Jay	*Cyanocitta cristata*
Scrub Jay	*Aphelocoma coerulescens*
Common Crow	*Corvus brachyrhynchos*
Great Tit	*Parus major*
Blue Tit	*Parus caeruleus*
Coal Tit	*Parus ater*
Lapp Tit	*Parus cinctus*
Marsh Tit	*Parus palustris*
Willow Tit	*Parus atricapillus*
Black-capped Chickadee	*Parus atricapillus*
Carolina Chickadee	*Parus carolinensis*
Tufted Titmouse	*Parus bicolor*
Plain Titmouse	*Parus inornatus*
Long-tailed Tit	*Aegithalos caudatus*

Common Bushtit	Psaltriparus minimus
White-breasted Nuthatch	Sitta carolinensis
Red-breasted Nuthatch	Sitta canadensis
Brown-headed Nuthatch	Sitta pusilla
Pygmy Nuthatch	Sitta pygmaea
Brown Creeper	Certhia familiaris
House Wren	Troglodytes aedon
Winter Wren	Troglodytes troglodytes
Plain Wren	Thryothorus modestus
Riverside Wren	Thryothorus semibadius
Carolina Wren	Thryothorus ludovicianus
Mockingbird	Mimus polyglottos
Catbird	Dumetella carolinensis
Brown Thrasher	Toxostoma rufum
Blackbird	Turdus merula
Robin	Turdus migratorius
Hermit Thrush	Hylocichla guttata
Eastern Bluebird	Sialia sialis
Goldcrest	Regulus regulus
Golden-crowned Kinglet	Regulus satrapa
Ruby-crowned Kinglet	Regulus calendula
Gray Shrike	Lanius excubitor
White-eyed Vireo	Vireo griseus
Red-eyed Vireo	Vireo olivaceous
Black-and-White Warbler	Mniotilta varia
Orange-crowned Warbler	Vermivora celata
Parula Warbler	Parula americana
Magnolia Warbler	Dendroica magnolia
Myrtle Warbler	Dendroica coronata
Audubon's Warbler	Dendroica auduboni
Black-throated Green Warbler	Dendroica virens
Blackburnian Warbler	Dendroica fusca
Bay-breasted Warbler	Dendroica castanea
Blackpoll Warbler	Dendroica striata
Pine Warbler	Dendroica pinus
Northern Waterthrush	Seiurus noveboracensis
Yellowthroat	Geothlypis trichas
Canada Warbler	Wilsonia canadensis
American Redstart	Setophaga ruticilla
House Sparrow	Passer domesticus
Redwinged Blackbird	Agelaius phoenicus
Common Grackle	Quiscalus quiscula
Brown-headed Cowbird	Molothrus ater
Plain-colored Tanager	Tangara inornatus
Bay-headed Tanager	Tangara gyrola
Rufous-winged Tanager	Tangara lavinia
Blue Tanager	Thraupis episcopus
Palm Tanager	Thraupis palmarum
Scarlet-rumped Tanager	Ramphocelus passerinii
Olive Tanager	Chlorothraupis carmioli
Red-crowned Ant-tanager	Habia rubica

Red-throated Ant-tanager	Habia guttaralis
Tawny-crested Tanager	Tachyphonus delatrii
Common Bush-tanager	Chlorospingus ophthalmicus
Sooty-capped Bush-tanager	Chlorospingus pileatus
Cardinal	Richmondena cardinalis
American Goldfinch	Spinus tristis
Rufous-sided Towhee	Pipilo erythrophthalmus
Bachman's Sparrow	Aimophila aestivalis
Slate-colored Junco	Junco hyemalis
Chipping Sparrow	Spizella passerina
White-throated Sparrow	Zonotrichia albicollis
Swamp Sparrow	Melospiza georgiana

VITA

Douglass Hathaway Morse was born on 20 July 1938 in Lewiston, Maine. He majored in biology at Bates College, Lewiston, Maine, where he was graduated in 1960 with the degree of Bachelor of Science. In 1962 he received the degree of Master of Science from the University of Michigan, having entered there in September, 1960. He enrolled at Louisiana State University in September, 1962. He is a candidate for the degree of Doctor of Philosophy in May, 1965.

EXAMINATION AND THESIS REPORT

Candidate: **Douglass Hathaway Morse**

Major Field: **Zoology**

Title of Thesis: **Biology of Mixed Foraging Flocks of Avian Species**

Approved:

George H. Lowery Jr.
Major Professor and Chairman

Max Goodrich
Dean of the Graduate School

EXAMINING COMMITTEE:

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H. B. Boudreaux

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Date of Examination:

6 May 1965